QUADRUPLE HYBRIDS IN THE F_1 GENERATION FROM *OENOTHERA NUTANS* AND *OENOTHERA PYCNOCARPA*, WITH THE F_2 GENERATIONS, AND BACK- AND INTER-CROSSES[1]

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TABLE OF CONTENTS

PAGE

INTRODUCTION 213
The F_1 hybrids from *Oenothera nutans* and *Oe. pycnocarpa* 220
Characters of the four hybrids of the F_1 generation compared with the parents 224
Correlation between hybrid constitution and relative state of sterility or fertility 237
The F_2 generations 241
Back- and inter-crosses of the hybrids *pycnella, nutella* and *tortuosa* 242
The behavior of *Oenothera nutans* and *Oe. pycnocarpa* compared with other wild species of Oenothera 247
Interpretations of splitting in the first generation 248
Selection of characters in the zygote versus Mendelian segregation 248
Is the production of these quadruple hybrids due to the mutating condition of one of the parents? 249
Stable and unstable dominance in the hybrids *pycnella, tortuosa* and *tortuella* 251
Multiple dominance in the F_1 generation of crosses between *Oenothera nutans* and *Oe. pycnocarpa* 255
SUMMARY 257
LITERATURE CITED 258

INTRODUCTION

One of the many interesting and remarkable features of the evening primroses of the genus Oenothera (section Onagra), is the large number of distinct genetic types in the species *Oenothera "biennis"*, as generally understood in North America. In many localities a superficial examination will reveal distinct types in the population of this "species".

[1] An account of three of the hybrids was presented before the American Phil. Soc. at its general meeting in April, 1914 (see ATKINSON 1914). This paper was accepted by the Zeitschr. f. ind. Abst. u. Vererb., and the proof was read in October, 1914, but the European war has probably prevented its publication. An account of the F_2 generations, and back- and inter-crosses, was presented at the general meeting of the Am. Phil. Soc. in April 1916. Only very brief abstracts of any portion of this work have as yet been published.

These types differ either in the character of the flowers, stems, foliage or rosettes, or in all combined. Certain types manifest great resistance to the attacks of certain fungi, especially to Peronospora. The juices of certain types are preferred by the tarnished plant bug. The seeds in some forms present striking differential characters.

In the vicinity of Ithaca, N. Y., as the result of a partial survey of a very small portion of territory, I have found a dozen different forms in the so-called *"biennis* alliance", which in cultivation have proven to be distinct types. The uniformity of character shown in the rosettes, as well as in the mature plants, in the population bred from each of these types, is remarkable, and dispelled the suspicion at first entertained that the different forms recognizable in the field might be merely fluctuating modifications in a very "variable" species. Some of them differ by so many characters and manifest such strikingly different genetic constitutions, that they evidently represent different specific types. Sev-

FIG. 1 FIG. 2

FIGURE 1.—*Oenothera nutans* Atkinson and Bartlett.
FIGURE 2.—The blend hybrid, *hybrida nutella* (n × p).

eral such distinct specific types have been isolated from the *Oenothera "biennis"* population in the vicinity of Ithaca. BARTLETT (1911, 1913) has isolated a number from several different localities in the United States, and DE VRIES (1913) had previously observed and gathered similar distinct types in this country.

This composite constitution of the *"biennis* alliance" in North America is reflected in the different concepts of this species in some of the manuals on North American botany, thus rendering it quite impossible, in some localities at least, to correlate any of the forms with the descriptions of *Oenothera biennis* in the manuals. The situation is further complicated by the fact that the true *Oenothera biennis* is probably that referred to by LINNAEUS from the sand dunes of Holland (see BARTLETT 1913, p. 48), where it is believed to be an immigrant from North America, though so far as I know the Holland type of *biennis* has never been observed in our country.

Besides the great number of morphologically different species and varieties in the *"biennis* alliance" in North America, with their characteristic genetic constitutions, there exists another remarkable peculiarity, noted also in other species of the genus, viz., the marked power which some of these types have to produce splitting in the F_1 progeny of certain crosses, while others lack it, or possess it only to a very limited degree. DEVRIES (1913) has clearly demonstrated this variability in splitting power of certain species of Oenothera.

During the summer of 1909, on a small area of an abandoned pasture, which I was developing as a private wild garden, just within the limits of the city of Ithaca, there were a number of self-sown evening primroses. No critical examination was made of them, but as I passed among them almost daily I finally became aware, perhaps by a process of unconscious differentiation, that certain individuals had red stems and red mid-veins of the leaves, while other individuals had green stems and white mid-veins. These were the only differential characters which attracted my attention that season, as I was not aware at that time of the fact that *Oenothera "biennis"* was a composite species embracing a large number of elements which breed as distinct species and forms. It occurred to me that it might be interesting to hybridize these forms for the purpose of observing the distribution of color in the hybrids and in their progeny. Cross pollinations were then made between two selected individuals, one of each type. But seed was obtained that year only from the green-stemmed individual fertilized by the use of pollen from the red-stemmed one.

Being absent from Ithaca during the summer of 1910, the seed was not sown until the spring of 1911. Seed from each parent, saved from protected flowers, was also sown. The young seedlings were transplanted from the seed pans to flats in the usual way and when of suitable size they were transplanted to the garden. They were not forced by planting early, and were therefore grown as biennials. During midsummer marked differences began to appear in the rosette leaves, which became very striking during the autumn. The rosette leaves of the parents differed by five or six characters, and it was evident that there were at least two hybrid types. The hybrid types, however, could not be very well determined because many of the rosettes were more or less severely attacked by the downy mildew (*Peronospora Arthuri*), while many of those of the green-stemmed parent were more severely injured.

The following season (1912) the plants came into flower. A critical study revealed further striking differences between the two parents. The differential characters relate to habit, leaves, stems, inflorescence, flowers, and seed pods, altogether some 25-30 characters being noted by which the two forms differed. The two forms were very distinct from *Oenothera biennis* as recognized by DEVRIES, BARTLETT and others, and were regarded as undescribed species. They were submitted to BARTLETT who confirmed this opinion and they were described as *Oenothera nutans* Atkinson & Bartlett, and *Oe. pycnocarpa* Atkinson & Bartlett. For a complete diagnosis of the two species the original descriptions (see BARTLETT 1913, p. 81) should be consulted, but a brief synopsis of the characters is given below.

All of the cultures were carried out in fairly rich garden soil and some tillage was given, enough to keep down weeds and to stir the soil several times, particularly during rosette development and during the spring of the second season. Under these conditions the full expression and strength of characters are realized. These characters relate to the habit and coloration of the adults; features of the rosettes, foliage and inflorescence. The habit and morphological characters are well shown in the photographs here reproduced. The measurements given are for the garden cultures.

Oenothera pycnocarpa. Habit: tall, 1—1.5 m; lower stem branches numerous, strict, not widely spreading, reaching about the middle of the main stem, main stem therefore with high over-top, tips nearly the same level; axillary rosettes over the middle and upper part of the main stem, or short flowering branches just below the main inflorescence.

Autumnal rosettes compact, the larger leaves (late summer and early autumn leaves) narrow, deeply cut over the basal half, furrowed, repand, white-veined, plain or only slightly buckled, no reddish spots. *Stems* green, (rarely tinged red on a portion of the sunny side), tubercles green. *Stem leaves* drooping, narrow, white-veined, slightly sinuate-toothed (lower leaves strongly so over basal portion), furrowed, plain, no red spots. *Inflorescence* long and dense; bracts green, slightly sinuate-toothed, longer than the flower buds, persistent, basal ones longer than the pods. *Petals* lemon yellow, cuneate, strongly emarginate, not plicate, edge plain, medium size, firm, not quickly wilting. *Fertility* high (pods with many viable seeds). *Plant* flowering for a long period and maturing late. See figures 5, 8 and 13.

FIG. 3

FIG. 4

FIGURE 3.—The selective hybrid, *hybrida pycuella* (n × p).

FIGURE 4.—The selective hybrid, *hybrida tortuosa* (n × p). The main stem is fasciated and has split into two branches, the height or over-top of the main stem is therefore probably not so great as it would have been if it were not for the fasciation.

Oenothera nutans. Habit: medium height, .75—1.00 m; lower stem branches numerous, spreading irregularly, reaching far above the middle of the main stem, main stem therefore with low over-top, tips at unequal heights, not terminating at the same level; axillary rosettes over the middle portion of the stem; short flowering branches at base of the main inflorescence. *Autumnal rosettes* compact, the larger leaves broad, sinuate-toothed over the basal portion, convex, not repand, red-veined, strongly crinkled, reddish spots in the autumn. *Stems* dark red, sometimes also the base of the inflorescence axis is red, otherwise the inflorescence axes are green; tubercles red, even over the green parts of the stem, rarely red on the young pods. *Stem* leaves broad, very slightly sinuate-toothed over the basal portion, flat or convex, red-veined, plain or somewhat crinkled, few or no red spots. *Inflorescence* medium length, dense, sometimes lateral; bracts usually pale green and caducous, except sometimes a few of the basal ones are green and persistent, small and shorter than the flower buds, edge plain. Petals chrome yellow, obovate, or scarcely emarginate, plicate, edge eroded, weak, soon withering, medium size, but larger than in *Oe. pycnocarpa. Fertility* high. *Plant* maturing early (in late summer or early autumn). See figures 1, 8 and 9.

Besides several minor deviations, of little consequence here, there is an important variation which should be taken into account and clearly understood. This variation consists in the production of annual individuals by biennial species. This is particularly liable to happen in artificial cultures, and sometimes is encouraged by the investigator for the express purpose of saving time. Where seeds are sown during the winter and the seedlings have reached some size by the time the growing season permits transplanting to the garden, the influence of the warm summer season on these more advanced seedlings may stimulate them to early stem growth so that they flower and fruit in a single season. In some cases a large percentage, or the total, of the culture may form annuals, while a small percentage, or none, pass on to the rosette form. Where the species contrasted have autumnal rosettes with strikingly different character composition, the annuals, in the case of some species, fall far short of presenting the full complexion of the specific character. This is true of the two species here studied as well as of their hybrids. The annual forms of *pycnocarpa*, produced in culture in 1913, and again in 1914 and 1915 came into flower early except those of one lot from a seven-carpeled pod in 1914. Those grown as annuals formed no mature rosettes. The later leaves of the rosettes, and the lower

stem leaves of these annual forms, were very strongly toothed over the basal portion, but did not approach the cut condition of the later leaves of mature autumnal rosettes.

If cultures are started in March or April, and the seedlings grown in 2-inch pots until they become pot-bound, all or a percentage may develop as true annual forms, depending on the way the cultures are handled. In the cultures of 1914, some individuals of *nutans* came into flower early in July, others in August, and a very few formed only rosettes which were quite well formed early in August, and characteristically mature in September.

Since the rosette leaves developed in late summer and early autumn attain a higher degree of morphological differentiation than the spring and early summer leaves, the complete life cycle and full expression of the species is not obtained when these species are grown as annuals. The annuals of biennial species reach the flowering and fruit period by short-circuiting the complete life history. They are really

FIG. 5 FIG. 6

FIGURE 5.—*Oenothera pycnocarpa* Atkinson and Bartlett.
FIGURE 6.—The blend hybrid, *hybrida nutella* (p × n).

short-circuit forms with paedogenic rosettes. Sometimes in greenhouse cultures seeds falling from ripe pods of a potted plant during the winter, germinate, and under the warm conditions of hothouse culture begin stem development early, omitting the rosette stage. Such short-circuit forms, in species where late summer and early autumn leaves of autumnal rosettes are strongly cut over the basal portion, and the stem leaves are only slightly cut, or toothed, suggest a variation in the leaves due to the influence of the changed environment, and thus may be misleading. The cycle has been shortened from early rosette leaves slightly cut to lower stem leaves slightly cut, omitting the late-formed strongly cut leaves of the mature rosette stage.[2] All gradations sometimes appear between the extreme short-circuit forms and those with the rosette stage complete, the degree of rosette development reached depending on the time at which stem development begins. So far as I am aware the conditions have not yet been analyzed which determine the time of stem development in these annual forms of biennial species.

THE F_1 HYBRIDS FROM *OENOTHERA NUTANS* AND *OE. PYCNOCARPA*

As already noted, the injury to many of the rosettes in the 1911 cultures of the cross *Oe. pycnocarpa* (green stem) × *Oe. nutans* (red stem), from the attacks of the Peronospora prevented a satisfactory analysis of the hybrid types. In the following year (1912) these biennial forms which were not seriously injured by the parasite came into flower. There were two distinct hybrid types. One of these appeared to be a blend, but the petals were more like those of *Oe. nutans,* though larger than those of either parent. It has been named *Oe. hybrida nutella.* It proved to be self-sterile. The other hybrid was selective, receiving certain characters from each parent and developing them to their full expression. The flowers were exactly like those of *Oe. pycnocarpa,* and it has been named *Oe. hybrida pycnella.* It is self-fertile to a very high degree.

Because of the injury to the rosettes parasitized by the Peronospora, the experiments were repeated. It was also desirable to study the reciprocal crosses between the two species. Therefore reciprocal cross-pollinations of the parents in the first generation of the garden cultures were made in 1912.

The seed of these reciprocal crosses, as well as of the two parents, was

[2] Exactly such short-circuit annual forms appeared in an undescribed species, No. 17 of my 1913 cultures, about 50 percent being short-circuit forms, while the remainder which came into flower in 1914 formed mature rosettes with leaves strongly cut over the basal half.

sown in seed pans during March 1913. When the seedlings were furnished with 4 or 5 leaves they were transplanted to flats, and then when of suitable size were transplanted to the garden in May. Some developed as annuals and began to flower in July, while others formed autumnal rosettes and did not flower until the season of 1914. Of the hybrids which came into flower during July and August it was evident that there were two distinct types, and these two types were identical with the two hybrid types obtained the previous year. Furthermore, these two hybrid types appeared on each side of the reciprocal crosses.

FIGURE 7.—The selective hybrid, *hybrida pycnella* (p × n).

In the seedling stage, as well as in the early rosette stage it was quite impossible to differentiate the parents except for occasional red spots in the leaves of the red-stemmed parent, and as the leaves became larger the mid-veins of this parent also began to show the red color. Likewise it was impossible to distinguish the hybrid types, either from each other or from either parent. But when the annuals began stem development it was possible to differentiate the parents and hybrid types from the character of the lower stem leaves, but not with such certainty as at the flowering period or in the well developed autumnal rosettes.

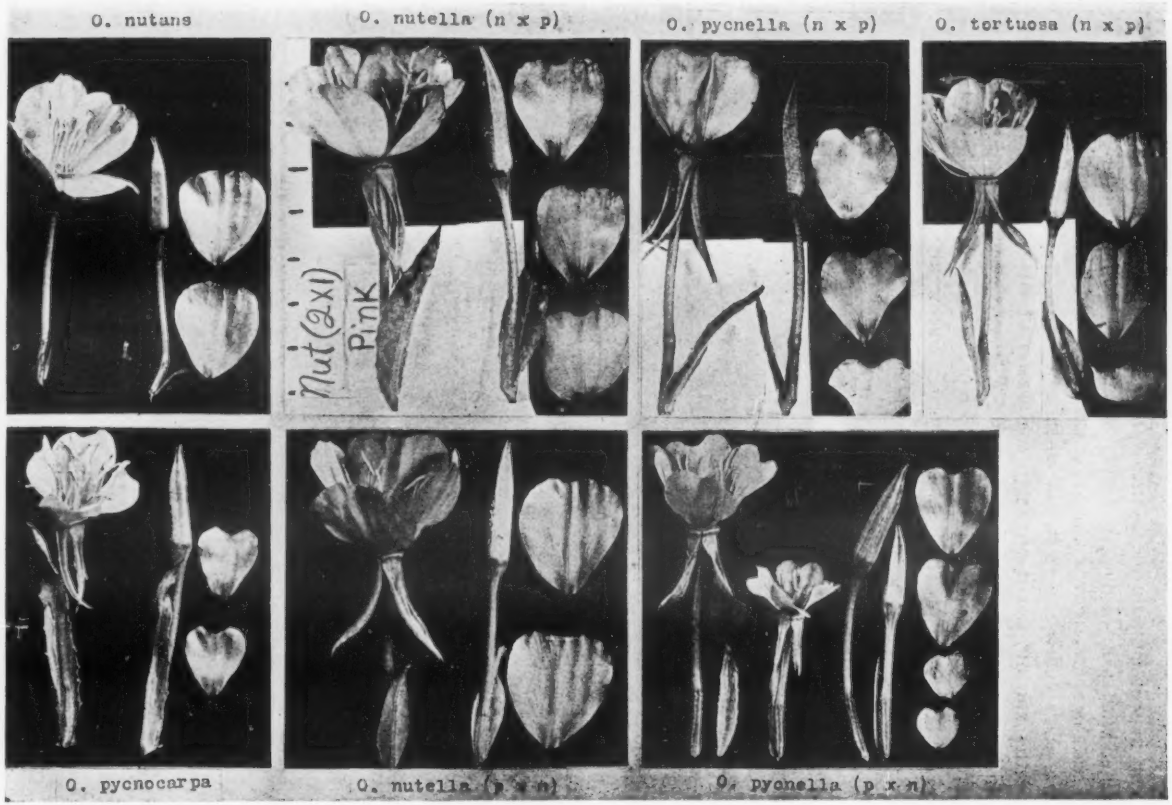

FIGURE 8.—Details of flowers and buds. The upper row contains *Oe. nutans* and three of the hybrid types when ***nutans*** is the mother. The lower row contains *Oe. pycnocarpa* and the two hybrid types when ***pycnocarpa*** is the mother. The parents are in the first column; the blend, ***hybrida nutella***, in the second column; the selective, ***hybrida pycnella***, is in the third column; and ***hybrida tortuosa*** (also a selective hybrid) is in the upper right-hand corner.

The remaining hybrid rosettes, those which did not proceed to stem development that season, could not be differentiated into types during July or early August. But as they approached the autumnal stage the new and larger leaves began to display the differential characters which permitted sorting into distinct types with a fair degree of accuracy, and when mature in September three distinct hybrid types were easily recognizable, the third type not producing annual forms that season. This third hybrid type is named *hybrida tortuosa*, because the mature autumnal rosette leaves are often more or less strongly twisted due to their narrow, convex, crinkled form. The following season (1914) the biennial individuals, those with the mature autumnal rosettes in 1913, came into flower, and *four* hybrid types in the F_1 generation of the cross were distinguished.[3] The fourth type had the rosette characters of the third but the stem color of the mature plant was green instead of red as in *tortuosa*. It is named *hybrida tortuella*.

Characters of the four hybrids of the F_1 generation compared with the parents

The principal characters of the F_1 hybrids may now be given. For the purpose of easy comparison the principal contrast characters of the parents are repeated.

Oenothera nutans. Rosette leaves broad, with a few rather prominent teeth over the basal part of the blade, convex, crinkled, red-veined; stems red; stem leaves spreading; petals obovate, overlapping, fluted, distal margin eroded and plain, quickly wilting; pods short, usually crowded; plants maturing early, very fertile; progeny very uniform.

Oenothera pycnocarpa. Rosette leaves comparatively narrow, deeply cut over the basal half of the blade, furrowed, repand, plain or somewhat buckled, white-veined; stems green; stem leaves depressed; petals cuneate, not meeting, not fluted, distal margin not eroded, notched, rather firm and wilting late; pods comparatively long, often crowded; plants maturing late, very fertile; progeny very uniform.

Oenothera hybrida nutella. A blend[4] hybrid. Rosette leaves flat, intermediate in width and edge characters between the two parents, the basal part of the mature autumnal leaves cut about half as deeply as in the *pycnocarpa* parent; stems pink; stem leaves spreading; petals larger than those of either parent, sometimes showing more of the *nutans* char-

[3] For the proportional numbers of these hybrid types in the reciprocal crosses see the tables 2 to 9.

hybrida tortuosa (also a selective hybrid) is in the upper right-hand corner.

acter, more rarely the *pycnocarpa* character dominates; absolutely self-sterile so far as tested, though pollen and egg cells are both functional in crosses with other forms; pods rather long, lax; plants maturing late, flowering for a long period.

Oenothera hybrida pycnella. A selective[4] hybrid. Rosette leaves broad, with a few rather prominent teeth over the basal part of the blade, furrowed, repand, plain; stem leaves spreading; stems green; flowers exactly like those of *Oe. pycnocarpa;* pods rather long, moderately dense; plants maturing early, very fertile; type fixed in the F_1 generation, breeds true, progeny very uniform.

Oenothera hybrida tortuosa. A selective hybrid. Rosette leaves

FIGURE 9.—Autumnal rosette of *Oenothera nutans.*

[4] The term "blend" hybrid is here used in the usual acceptation of the term. The allelomorphic factor pairs blend so that a form intermediate between the two appears. The term "selective" hybrid applied to the three other hybrids of the F_1 has reference to the fact that only one factor of each homologous pair is selected for expression in a given hybrid, from those in the F_1 zygote, the other factors being subordinated. The factors selected come from both parents.

comparatively narrow, deeply cut over the basal half of the blade, convex, crinkled, red-veined, often more or less twisted (probably a result of the tension from strong convexity and crinkledness of the narrow leaves); stems red; stem leaves convex, depressed, a few rather strong, distant teeth over base of blade; flowers exactly like those of *nutans;* pods short, dense (or crowded) like those of *nutans;* plants maturing late, very fertile; type fixed in the F_1 generation, breeds true; progeny very uniform.

Oenothera hybrida tortuella. A selective hybrid. This hybrid appears to have all the characters of *hybrida tortuosa* in the first generation, except the red stem, a *nutans* character, *hybrida tortuella* having the green stem of the parent *pycnocarpa;* very fertile; type not fixed in the F_1 generation, since in the F_2 generation it breaks into a number of types

FIGURE 10.—Rosette of blend hybrid *nutella* (n × p). Note the intermediate width and edge character of the leaves.

showing great variations. This fourth hybrid appears in very small numbers compared with the others.[5]

A single individual of *hybrida tortuella* appeared in the 1913-14 cultures. In the autumn of 1913 its rosette was classed as a *tortuosa*. It caused considerable surprise in 1914 when it came into flower that its stem should be green, since I had forecast a red stem for all the plants with *tortuosa* rosettes.

The photographs reproduced here present in graphic form nearly all

FIGURE 11.—Rosette of selective hybrid, *hybrida pycnella* (n × p). Observe the broadness and toothedness of the *nutans* leaves.

[5] The plants were not grown in large enough numbers to determine whether or not there is any regularity in the ratios of the different hybrid types appearing in the first generation. In the cross *nutans* × *pycnocarpa* (1913 culture) there were 108 plants in the garden culture. Of these 35 were annual *nutella*, and 10 were annual *pycnella*, 21 *tortuosa* and 1 *tortuella*. Of the reciprocal cross (*pycnocarpa* × *nutans*) only 51 plants were grown in the garden. Of these 4 were annual *nutella*, 9 were annual *pycnella*. There were 38 which formed autumnal rosettes, 36 *pycnella* and 2 *nutella*.

the characters of the two parents and their four hybrids. The fact that the parents differ by so many strong contrast characters, the majority of which under normal culture are so clear-cut and strikingly different in the two parents, permits a very satisfactory study of the transmission of the characters, and their composition in the F_1 hybrids.

The habit of the plants is shown in figs. 1 to 7, all from biennials. Figure 1 represents *nutans,* and figures 2 to 4 show three of the hybrid types of the cross *nutans* × *pycnocarpa;* figure 2 is the F_1 blend hybrid,

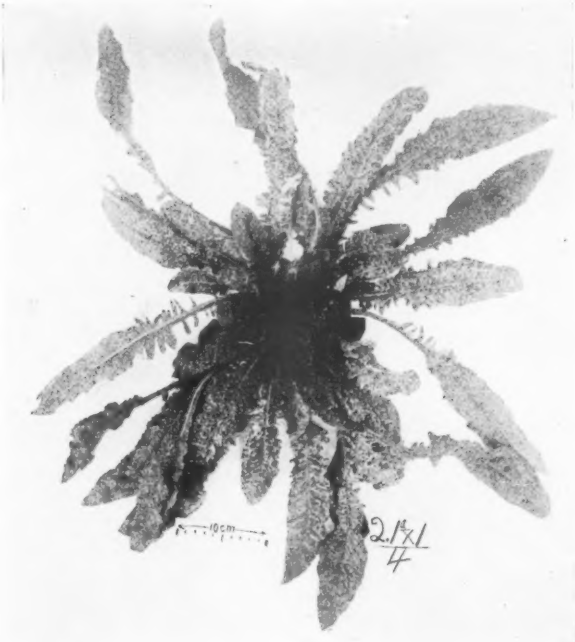

FIGURE 12.—Rosette of selective hybrid, *hybrida tortuosa* (n × p). Note the narrowness and cutness of *pycnocarpa* and the crinkledness and convexity of *nutans* in the leaves.

nutella; figure 3 the green-stemmed F_1 selective hybrid, *pycnella,* and figure 4 the red-stemmed F_1 selective hybrid, *tortuosa.*

In figure 8 are presented details of the inflorescence.[6] The differences

[6] It was rather late in the season when the flowers of *nutans* and *pycnella* (p × n) were photographed, and the bracts were not quite so large as the earlier ones.

in the petal characters are striking. The upper row contains *nutans* at the left, and then follow in order three of the hybrid types (*nutella, pycnella* and *tortuosa*) when *nutans* is the mother. The lower row contains *pycnocarpa* at the left, and two of the hybrid types (*nutella* and *pycnella*) when *pycnocarpa* is the mother. *Tortuella* is not shown, its

FIGURE 13.—Rosette of *Oenothera pycnocarpa.*

flowers being like those of *tortuosa.* The petals of *tortuosa* are clearly those of *nutans,* and the petals of *pycnella* are clearly those of *pycnocarpa.* The petals of *nutella* are often very like those of *nutans,* particularly as regards the plaited character and oboval form. They are, however, larger than those of *nutans.* The emargination is more pronounced, showing more of the *pycnocarpa* character. Sometimes the plaited character is not so pronounced, as is evident in the photograph of *nutella* (n × p). But in many examples the plaited character is very evident. While, therefore, the petals of this blend hybrid (*nutella*) more strongly resemble those of *nutans,* they are modified by those of *pycnocarpa,* the blend in the petal characters being less striking than in the vegetative characters.

The rosettes of *nutans* × *pycnocarpa* are reproduced in figures 9 to 12; those of *pycnocarpa* × *nutans* in figures 13 to 15. Figure 9 is the mother *nutans;* figure 10 is the F_1 blend, *hybrida nutella.* The *hybrida nutella* rosette of the reciprocal cross (*pycnocarpa* × *nutans*) is shown in figure 14. By a comparison with the rosettes of the parents (for the

FIGURE 14.—Rosette of the blend hybrid, *hybrida nutella,* from the cross *pycnocarpa* × *nutans.*

rosette of *Oe. pycnocarpa* see figure 13), the blending of the characters, wideness with narrowness, and cutness with toothedness, is very evident.

In figure 11 is shown a rosette of the F_1 selective, *hybrida pycnella,* from the progeny when *nutans* was the mother, and in figure 15 the same form when *pycnocarpa* was the mother. The two have the same composition of characters, but *pycnella* (p × n) has fewer leaves, selected because the leaf detail could be better represented in the photograph. The photograph shows the selection of the width and toothed character from *nutans.* Furrowedness and repandness come from *pycnocarpa,* but are

not shown well in the photograph. At the time the photographs were made furrowedness had not been recognized as a character and considerable effort was made to flatten the leaves down so that the edge characters would appear to better advantage.

In figure 12 is the F_1 selective *hybrida tortuosa*. This is as yet represented only from the progeny when *nutans* is the mother. It has not yet appeared in the cultures of *pycnocarpa* × *nutans*. This is quite a remarkable rosette. The larger leaves have the narrowness and cutness of *pycnocarpa*, the crinkledness and convexity of *nutans*, all these characters being clearly represented in the photograph. It has also the red-veinedness of *nutans*.

FIGURE 15.—Rosette of selective hybrid, *hybrida pycnella*, from the cross *pycnocarpa* × *nutans*.

In diagram 1 the principal characters which have been studied, are tabulated in such a way as to show the blending of the contrast characters of the two parents in the F_1 *hybrida nutella*, and also the sorting of

characters from the two parents with their recombination into new complexes, or mosaics,[7] in the F_1 selectives, *hybrida pycnella* and *hybrida tortuosa*. In the upper line are arranged the characters of *nutans*, in the lower line those of *pycnocarpa*, while in the middle line are arranged those of *hybrida tortuosa*, *hybrida nutella* and *hybrida pycnella*. The lines indicate the source and distribution of characters.

The abbreviations in the diagram are explained in table 1. *Hybrida tortuella* had not been detected when this diagram was made. But its phenotype in the F_1 is so like that of *hybrida tortuosa* (but having a green stem instead of the red stem of *tortuosa*) it is better to not complicate the diagram by its introduction.

As seen by an examination of diagram 1 there is a distinct linking or association, of certain factors in their transmission to the F_1 selective hybrids, *pycnella* and *tortuosa*. There is a splitting of the total factor composition of certain members of the plant body. The splitting, however, occurs almost entirely *between* factors, not *through* them, so that certain factors, or groups of factors, are transmitted entire to one or the other of the F_1 selective hybrids. Examples of this linking or association of characters are as follows: First, color characters; second, petal characters; third, broadness and toothedness of rosette leaves; fourth, narrowness and cutness of rosette leaves; fifth, crinkledness, convexity and red-veinedness of rosette leaves; sixth, plainness, furrowedness and white-veinedness of rosette leaves (in *hybrida pycnella* the mid-veins of the leaves are often tinged with red). The linked characters are inherited as follows by the two F_1 selectives, *pycnella* and *tortuosa*:

In *hybrida pycnella* the habit is taken from *nutans;* the rosettes take the broadness and toothedness of the leaves from *nutans;* the furrowedness, repandness and plainness of the leaves come from *pycnocarpa;* the green stem and green tubercles come from *pycnocarpa;* width and edge character of stem leaves come from *nutans;* the size and persistency of the bracts are derived from *pycnocarpa;* all the petal characters come from *pycnocarpa*. It will be noted that the green stem and petal characters come from *pycnocarpa*, but it may not be a case of linking between petal characters and stem color, other than that of their association in the parent *pycnocarpa*.

In *hybrida tortuosa* the habit comes from *pycnocarpa;* the rosette leaves take the narrowness and cutness from *pycnocarpa;* the convexity, crinkledness and red-veinedness from *nutans;* the red stem and red tubercles from *nutans;* width of the stem leaves comes from *nutans*, but

[7] These mosaics are of a different kind from those described by BLARINGHEM (1913).

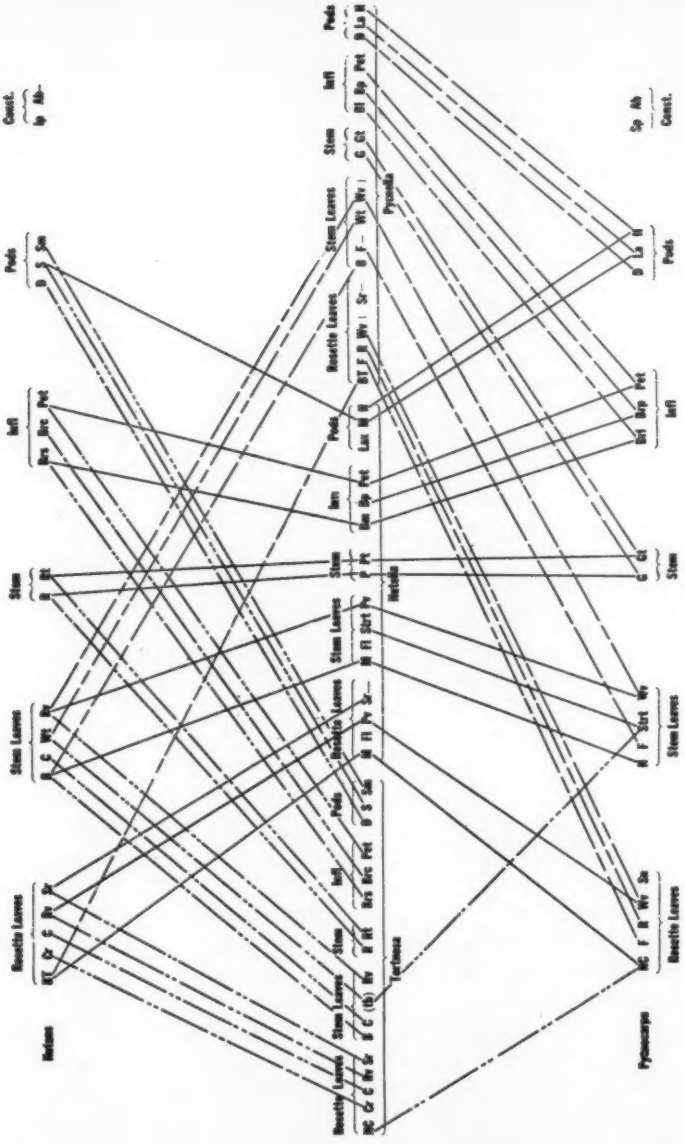

DIAGRAM 1.

TABLE 1

Key to the abbreviations used in diagram 1

	Nutans	*Tortuosa*	*Nutella*	*Pycnella*	*Pycnocarpa*
Rosette leaves	BT = broad and toothed Cr = crinkled C = convex Rv = red-veined Sr = spots red	NC = narrow and cut Cr = crinkled C = convex Rv = red-veined Sr = spots red	M = medium broad Fl = flat Pv = pink-veined Sr = some red spots	BT = broad and toothed F = furrowed R = repand Wv* = white-veined or pink-veined Sr = sometimes red spots	NC = narrow and cut F = furrowed R = repand Wv = white-veined Sn = spots none
Stem leaves	B = broad C = convex Wt = weakly toothed Rv = red-veined	B = broad C = convex (tb) = strongly and distantly toothed over base Rv = red-veined	M = medium broad Fl = flat Strt = strongly toothed Pv = pink-veined	B = broad F = furrowed, but not usually strongly so Wt = weakly toothed Wv+ = white-veined or pink	N = narrow F = furrowed Strt = strongly toothed Wv = white-veined
Stem	R = red Rt = red tubercles	R = red Rt = red tubercles	P = pink Pt = pink tubercles	G = green Gt = green tubercles	G = green Gt = green tubercles
Inflorescence	Brs = bracts small Brc = bracts caducous Pet = petal characters	Brs = bracts small Brc = bracts caducous Pet = petal characters	Bm = bracts medium Bp = bracts persistent Pet = petal characters	Bl = bracts large Bp = bracts persistent Pet = petal characters	Brl = bracts large Brp = bracts persistent Pet = petal characters
Pods	D = dense S = small Sm = smooth	D = dense S = small Sm = smooth	Lax = lax M = medium size H = hairy	D = fairly dense La = large H = hairy	D = dense La = large H = hairy
Constitution	Ip = immune to Peronospora Ab = attacked by bugs slightly				Sp = susceptible to Peronospora Ab+ = attacked by bugs

the edge character is different from either parent; the size and caducous character of the bracts are derived from *nutans;* all the petal characters come from *nutans.* In the mature state, when rosette leaves are not present, *tortuosa* resembles *nutans* very strongly, the habit, drooping of the leaves, and edge character of the stem leaves being the only differential characters in this stage. There are a few rather prominent and distant teeth on the base of the blade,[8] a very different character from the rather regularly serrate leaves over the middle and upper part of the stem of *pycnocarpa,* and the nearly plain edge of the stem leaves of *nutans.*

In *hybrida tortuella* the phenotypic characters of the F_1 are derived as in *tortuosa,* but instead of receiving the red stem of *nutans,* it takes the green stem of *pycnocarpa.* There is here a crossing over of stem color and flower character as compared with the two other selective hybrids.

While all the contrast vegetative characters possessed by the two parents are transmitted, each in its entirety, to the two F_1 selectives, some to *pycnella,* the others to *tortuosa,* the F_1 blend, *hybrida nutella,* inherits all, or a very large proportion of the contrast characters of the two parents. In such a case it is impossible for both characters of the "allelomorphic pair" to express themselves in their completeness. Each is modified by the other member of the pair so that an intermediate state between the two contrast characters is attained. The "allelomorphs" blend. In the rosettes, the broadness and toothedness of *nutans* blend with the narrowness and cutness of *pycnocarpa;* the convexity and crinkledness of *nutans* blend with the furrowedness of *pycnocarpa* and the leaves are flat or nearly so. There are no real intergrading forms between the three hybrids, though each one shows slight fluctuations. The red color of the stems and tubercles of *nutans* blend with the green of *pycnocarpa* and an intermediate state of coloration (pink) results. The small bracts of *nutans* blend with the large ones of *pycnocarpa* and bracts of an intermediate size appear on *nutella.*

The F_1 blend hybrid (*nutella*) presents a very interesting case of sterility. When the inflorescence is covered with paper bags, or other screen, to prevent insects from bringing foreign pollen to the stigma, no seeds are developed. Though the pods often attain a considerable size and give the impression that seed is being formed, they are found to be

[8] The few rather prominent teeth over the base of the stem leaves recalls the same feature of the lower stem leaves of the parent *pycnocarpa,* but the stem leaves of *tortuosa* with this character have a more extensive distribution on the stem than is the case in *pycnocarpa.*

hollow, and finally die. This is not due to a failure in pollination, for, like the parents, and others of the smaller-flowered oenotheras, pollination takes place in the bud. In the summer of 1912, when it was discovered that protected flowers were not setting seed, a large number were hand-pollinated. Not only was pollen from the same flower used in some cases, and in others pollen from different flowers of the same individual, but cross-pollinations between different individuals were also made. No seed formed. During the summer of 1913 a much larger number of hand-pollinations were made. Several inflorescences were also protected by covering with paper bags. In no case did seed develop. A large number of hand-pollinations were again made in 1914, using not only *nutella* (n × p) but *nutella* (p × n) in reciprocal cross-pollinations. No seed was formed. The same results were obtained in 1916.

The sterility of the blend hybrid (*nutella*) is not due to sterility of the pollen or egg cells. Flowers which are unprotected, if visited by bees which have access to the parents or other species, growing in proximity, set an abundance of viable seed. When hand-pollinated, using pollen from either parent, from *hybrida pycnella, hybrida tortuosa,* from *Oe. grandiflora, Oe. Lamarckiana,* and some other species, an abundance of viable seed is formed. The pollen is well formed, showing a small, and no greater, percentage of poor grains than either of the parents. It is effective when placed on the stigma of either parent, on *hybrida pycnella* and *hybrida tortuosa,* on *Oe. grandiflora, Oe. Lamarckiana,* and other species.

The cause of the sterility of *hybrida nutella,* therefore, has not been determined. But it may be due to a lack of correlation in certain of the physiological processes among the blended "factors," or characters, inherited from the two parents. Or it may be due to a lack of blending among some of the homologous characters, structures or physiological processes or parts of the inflorescence. If a complete and equal blending of all homologous factors for the inflorescence took place, it may be that the reproductive processes would present as high a degree of efficiency as the vegetative processes have. That the phenomenon of blending of all the homologous factors for the inflorescence does not take place is shown by the petals, which are far more like those of *nutans* than of *pycnocarpa.* The blending of certain parental characters in the inflorescence, the taking over of others in their entirety from one parent with the exclusion of their homologues, and possibly the incomplete blending or unequal sharing in the union of others may produce an organization ineffective for the reproductive processes. Certain of the "qualities" or

properties combined in the egg, or pollen, or both, may lack the reciprocal influences necessary to a union of sperm and egg, although sperm and egg are effective in other combinations. It is also possible that certain physiological properties may retard the growth of the pollen tube when the flowers are selfed, but may not be effective against the growth of the tube from foreign pollen. Some preliminary studies indicate that the pollen tube does not grow rapidly enough down the style to reach the egg in time.

Whatever may be the nature of the lack of a reciprocal working of the reproductive mechanism in *hybrida nutella* it can not be attributed to irregularities in the meiotic division preceding the formation of the pollen, such as have been shown by JUEL (1900, p. 639-641) to take place in *Syringa Rothomagensis* (a hybrid of *S. vulgaris* and *S. Persica*, according to FOCKE 1881, p. 255), where typical mitotic figures are rare in the first division of the gonotokonts. In the atypical cases a process intermediate between mitosis and constriction occurs, a number of chromosomes appear to go to the daughter nuclei undivided, some are left in the cytoplasm. He suggests that there is a lack of mixing of the nuclear substance. Irregularities have also been shown by ROSENBERG (1903, 1904, 1909) in a hybrid between *Drosera rotundifolia* and *D. longifolia*, where there is a difference in the number of chromosomes in the two parents; by CANNON (1903, p. 133) in a Gossypium hybrid (*G. Barbadense* × *herbaceum*), where some pollen mother cells divide normally, others abnormally; and by METCALF (1901, p. 109) in Gladiolus hybrids, where two spindles were observed, presumably due to a repulsion between the paternal and maternal chromosomes, so that they remain in separate groups. These and similar abnormalities in meiotic division may explain the sterility of pollen in certain hybrids. STRASBURGER (1904, p. 609) makes the interesting suggestion that the difficulties resulting in the formation of imperfect pollen occur in synapsis of the heterotypic division.

But, as stated above, this can not account for the sterility of *hybrida nutella*, unless during synapsis (or other critical moments in the formation of the gones) there is an association of physiological "properties" or "tendencies" in the pollen and embryo sac of such a nature as to prevent the reciprocal working of the sperm and egg of *hybrida nutella* when brought together, but permits reciprocal working when either sperm or egg mates with a germ cell of related forms.

The F_1 hybrids of *Nicotiana Forgetiana* crossed with *N. alata grandiflora* are individually self-sterile according to EAST (1915, p. 80) as are

the F_2, F_3 and F_4 generations. But cross-fertility is high between different individuals of each generation, or between individuals of different generations. The rate of growth of the pollen tubes down the style is so slow that they do not reach the ovary before the flower wilts, when individual plants are selfed. But in cross-pollinations between different individuals of any generation, the growth of the pollen tube is accelerated and reaches the ovary in time to carry the sperm cell to the egg. The self-sterility of individuals is explained by EAST on the ground that the protoplasms of the sex members are alike; and the pollen therefore lacks the kind of enzymes needed to call forth the secretion of a hexose sugar in the style which gives the direct stimulus to the pollen tube in those cases where its growth is accelerated.

The blend hybrid, *Oe. hybrida nutella*, is thus a striking instance of an intermediate hybrid which is totally self-sterile so far as determined. Not only are individual plants sterile, but all members of the race, whatever their origin (i.e. from either side of the reciprocal crosses of the parents), show cross-sterility when bred *inter se*.[9] But this sterility is not due to an impairment of the fertile condition of either the pollen or egg cells. The self-sterility may be due to a too great likeness of the protoplasm of the sex members as EAST suggests for the individual self-sterility of the Nicotiana hybrids. The rate of growth of the pollen tube in *nutella* has not been definitely determined. Some preliminary studies suggest that it grows too slowly to reach the ovules in time.

It does not seem clear how the protoplasm of the sex members of *hybrida nutella* could be any nearer alike than those of each of the parents since the parents are very likely what DEVRIES calls isogamous species. Furthermore the parents, like most small-flowered oenotheras, have a very long historical background of close inbreeding, which according to EAST's suggestions should result in protoplasmic identity in the sexual members. Close and long-continued inbreeding in plants at least, does not in all cases lead to complete sterility resulting in an incompatibility between the germ cells, though it may largely account for partial sterility of the pollen. The somatic cells carry all the factors of the two germ cells, but at the time of the development of the reproductive structures there is a differentiation into maleness and femaleness, manifest in many cases by differentiation in form. Probably also physi-

[9] In 1916 I had in culture a new race of *nutella* from a cross between *Oe. nutans* of the third generation and a feral individual of *Oe. pycnocarpa*. Cross-pollinations were made between this race of *nutella* and that from crosses between the 3rd generation of the original parents. No seed was formed.

ological differentiation takes place resulting in the formation of different enzymes, etc. The mere fact then, of the coming together of the protoplasm of *nutans* and *pycnocarpa* into the blend *hybrida nutella* would not make the protoplasm of its sex members any more alike than is the case in either of its parents. But the lack of complete blending in certain features of the inflorescence and flowers may prevent certain physiological differentiations necessary to establish a state of compatibility sufficient to permit the coming together and union of the germ cells.

There is another feature which should be considered. The pollen and egg cells may be overloaded with active factors since the sperm and egg cell each carry all or nearly all the factors of both parents of the cross in an active state. If there is physiological incompatibility between sperm and egg, as I am inclined to believe, can it be that this overload of factors, all tending to express themselves as they do in this blend hybrid, has anything to do with this incompatibility?

Correlation between hybrid constitution and relative state of sterility or fertility

The three hybrids present an interesting correlation between their hybrid constitution and their relative state of sterility or fertility. *Hybrida nutella* inherits all the factors of its parents. All the factors are active and only a mean between the homologous characters results. The vegetative characters are a blend. Certain flower structures are combined in such a way as to produce an inefficient reproductive machine and sterility results, although both pollen and egg cell are efficient in other combinations. In *hybrida pycnella* on the other hand, while "inheriting" in its egg cell all of the same factors, there is selected an effective combination of active factors which do not blend. It reaches a very high state of efficiency in its reproductive structures for it possesses a very high degree of fertility. The same can be said of *hybrida tortuosa* in which different factors are selected from the same "inheritance" in its egg cells,—factors which are complementary to those present in *hybrida pycnella.*

Another feature in which the annual forms of *pycnella* differ from either parent is the less dense inflorescence. Consequently the pods are not so crowded as they are in either parent grown as biennials, though the pods are large and crowded with seeds. So far as the parents are concerned, the biennial forms are stocky, and there is a great tendency to fasciation in the stocky individuals on rich soils, much more so in *pycnocarpa* than in *nutans.* No fasciation has been as yet observed in

pycnella, whether annual or biennial forms. While the petals of *pycnella* are usually of the same size as those of *pycnocarpa,* and smaller than those of *nutans,* under certain conditions, not yet determined, they are larger even than those of *nutans,* in size sometimes approaching those of *nutella.*

In the F_1 blend hybrid, *hybrida nutella,* besides the sterility resulting from the lack of correlation in some part of the reproductive machinery, there are some striking modifications in the inflorescence. As already stated, the petals are larger than those of *nutans,* which in turn has larger petals than *pycnocarpa.* The flower buds also average longer, and the spread of the flower is greater.[10] The cause of this progression in the size of the flower has not been determined. It is not accompanied by increased size of other members of the plant body. Possibly it may bear some correlation to the self-sterility, since certain forms of sterility in plants are sometimes accompanied by more showy flowers. It is known also that some hybrids are larger than either parent, but the increase in size here relates only to parts of the flower. The stigma does not over-top the stamens as in many of the large-flowered open-pollinated oenotheras.

Another striking modification in *hybrida nutella* is the lax inflorescence and the consequent lax relation of the pods. This is a characteristic of the annual as well as of the biennial forms.

While *hybrida pycnella* matures early, the annual forms very early, *hybrida nutella* matures late. The annual forms of *nutella,* even though they flower early in some seasons, usually continue to flower until killed by frost in November. It would seem therefore that the earliness of *nutans* is not only inherited by *pycnella,* but also that a progression in this quality has taken place so that the earliness of maturity is intensified. On the other hand, the lateness of *pycnocarpa* is inherited by *nutella* and there appears to have occurred a progression of the quality of lateness in this hybrid.

In *hybrida tortuosa* the edge character of the stem leaves is peculiar, the basal half having fewer teeth than either parent, over the same extent. *Tortuosa* is the only one of the hybrids thus far which may be fasciated, all of the biennial individuals, except one, presenting this character in a marked degree, so that the over-top of the main stem is

[10] In *Oe. pycnocarpa* the spread of the open flower is 20-35 mm, the petals average about 15 × 15 mm. In *Oe. nutans* the spread of the open flower is 35-42 mm; the petals are 18-32 mm long × 15-20 mm broad. In *Oe. hybrida nutella* the spread of the open flower is 50-55 mm; the petals are 20-25 mm × 20-22 mm broad.

not what it otherwise would be. *Tortuosa* also continues to flower longer than *nutans,* this character as well as that of fasciation probably being drawn from *pycnocarpa.*

Difference in habit between annual and biennial forms

The habit of the annual forms of the two hybrids, *pycnella* and *nutella,* is shown by my cultures thus far to be quite different. The plants are lower in stature, and this is true of annual forms of *pycnocarpa* and *nutans.* The lower branches are more spreading, especially those arising in the axils of the rosette leaves, but to some extent also, the lower stem branches. The wider-spreading branches with the lower stature gives to the plant quite a different habit from that of the biennial forms. This variation in form must be taken into account in any comparison of the hybrids with their parents. The habit varies also according to the time in the season at which stem development begins. The earlier in the season stem formation and branching begin, the more nearly normal will the habit be, according to my observations. If stem development is postponed until August or September the lower branches diverge at a wider angle, and often grow for some distance nearly or quite parallel with the surface of the ground, the free end usually curved more or less strongly upward. Many of these branches may be as long or longer than the central axis, but the upward curving tip may not reach the same height as the main stem. This peculiarity has been observed in *hybrida pycnella, hybrida nutella* and the cultures of *pycnocarpa.*

Among the 1913 cultures of *pycnocarpa,* where seeds were sown in the greenhouse during March, and the seedlings later transplanted to the garden, in one lot from a seven-carpeled pod only 2 out of 120 plants formed stems and flowers during the first season. Stem development began late in the season, toward the middle or last of August. In one plant the main stem was inclined at an angle of about 45°, and the branches arising from the base of the stem were wide-spreading. In the other plant the main stem grew parallel with the ground and was so rigid that it could not have been brought to the erect position without breaking.

In another race of Oenothera from Ithaca, No. 17 of my cultures, a large percentage of annual forms occurred in transplanted seedlings in 1913. Some of these began stem development early enough to mature seed. The branching of these forms was near the normal. But those which began stem development from about the middle of August presented a wide departure from the normal, due to growth of the lower

branches nearly or quite parallel with the surface of the ground, and at a distance from the main axis of 3-5 dm then curved upward. In another species from Ithaca, *Oenothera angustissima* GATES (1913), in my cultures of 1913 a very small percentage began stem development. Two plants came into flower in September. The branches were somewhat more wide-spreading than in the normal forms. Two others began stem development in September forming three or four stems each. None of these stems grew erect. All were prostrate and applied closely to the ground. During the latter part of September and October a dense rosette was formed at the tip of each of these prostrate branches, but no roots had formed. The plants with a large central rosette, and several smaller ones on prostrate stems 2-3 dm from the central rosette presented a very peculiar appearance. This same phenomenon has been observed in other species where stem development begins late.

These variations are epigenetic. They indicate a wide range in the morphological complex, among the individuals of certain species, races or hybrids. The amplitude of this variation is linear, i.e., it extends along the line of the life cycle which becomes short or long, simple or complex, according to epigenetic conditions. But the lateral variations or fluctuations do not meet nor transgress the limits between the species, races or hybrids.

What all of the conditions are which influence this variation in the length of the life cycle, and the lesser or greater degree in the full expression of the maximum characteristics, is difficult to determine. For example, it is difficult to judge the stimulus which determines the beginning of the stem development in the annual forms, which in some cases may occur at almost any time during the season. But when stem development begins, it appears to serve as a stimulus which checks the further development of the rosette, so that the rosettes are arrested in development at different periods. Soil conditions such as fertility, moisture content, etc., probably play a part. The formation of wide-spreading branches, particularly branches which grow for a considerable distance nearly parallel with, or on the surface of the ground, appears to bear some relation to temperature, especially to the seasonal cold of late summer and autumn.

In addition to the morphological evidence that there are no intergrading forms between the hybrids, very strong evidence is furnished by the high state of fertility in *hybrida pycnella* and *hybrida tortuosa,* which practically show no variability in this respect; and the quite complete self-sterility of *hybrida nutella.*

THE F_2 GENERATIONS

The behavior of these hybrids in the F_2 generation has been studied in all except *hybrida nutella,* which is self-sterile. Thus far the F_2 is obtained only when the hybrid is pollinated by some other form or species. *Hybrida pycnella* and *hybrida tortuosa* are fixed in the first generation, and therefore breed true, the F_2 generation being exactly like the F_1. They will probably continue to breed true in succeeding generations (*pycnella* has been tested to the 3rd generation). In this respect these two hybrids follow the general rule applying to most of the hybrids in the genus Oenothera (section Onagra) as discovered by DEVRIES (1903, 1911, 1913).

The behavior of the fourth hybrid in the 2nd generation is very peculiar. The F_2 generation of *hybrida tortuella* was first obtained in the summer of 1915 in a number of plants which were grown as annuals: the mature rosette stage was therefore not obtained. The plants presented great variations, apparently none of them assignable strictly to any of the types represented by the two parents or the other three hybrids. No special study was made of these different types partly because the number of other cultures requiring attention made impossible the necessary critical examination of these new types. The result was such a surprising contrast with the behavior of the other three hybrids, it seemed desirable that the culture should be repeated. This was deemed important not only for the purpose of eliminating the possibility of an error in the 1915 cultures, but also that the complete life cycle might be studied in cultures of the plants grown as biennials. Several individuals of the *hybrida tortuella* appeared in the 1915 F_1 generations of reciprocal crosses between *nutans* and *pycnocarpa,* so that there was an opportunity of studying the behavior of this hybrid from both sides of the cross. Flowers were not bagged to save protected seed until quite late in the season. The amount of seed saved was small. As a result of this together with rather scant germination, probably because of immaturity, the number of seedlings obtained was small.

The young plants in 2½-inch pots, bearing 4-5 leaves, were transplanted to the garden near the middle of July 1916. During August the rosettes began to show differences. By September the rosettes were well formed and the variations were very striking. The variations relate to size of the rosette, width of the leaf, edge character, color of the midvein, form, crinkledness, etc. In 23 rosettes 9 different types are represented, only one of them approaching the rosette character of *hybrida tortuosa.* These different types of rosette have been photographed and

noted. The further account of them is reserved until the mature plants can be studied in 1917.

BACK- AND INTER-CROSSES OF THE HYBRIDS *PYCNELLA, NUTELLA* AND *TORTUOSA*

Further experiments on the interaction of the "factors" present in *Oenothera nutans* and *Oe. pycnocarpa* were undertaken by making all the possible back- and inter-crosses of the three hybrids, *pycnella, nutella* and *tortuosa.* The fourth and rare hybrid, *tortuella,* was not included in these experiments for the reason that *tortuella* was at first supposed to be merely a green-stemmed form of *tortuosa,* in which the factor for red stem color was temporarily suppressed, and that it might appear again in the F_2. It was only after the completion of the back- and inter-crosses of the three other hybrids, that the discovery was made, that the genotypic constitution of *tortuella* was fundamentally different from that of *tortuosa,* resulting in a breaking up into numerous types in the F_2 generation. Some preliminary cultures were made in 1914. These were repeated in 1915 along with the cultures of the remaining back- and inter-crosses.

From the cultures of 1914 it was learned that in the reciprocal back-crosses of *pycnella* with *pycnocarpa,* only one type appeared in the progeny. When *pycnocarpa* was the mother and *pycnella* the pollen parent, the entire progeny was identical with *pycnella.* When *pycnella* was the mother and *pycnocarpa* was the pollen parent, all the progeny was identical with *pycnocarpa.* That is, in the reciprocal crosses between *pycnocarpa* and *pycnella* patrocliny prevailed. But when *nutella* was used in any of the crosses, splitting into two or more types usually occurs. The selective hybrid *pycnella* inherits the greater number of its characters from the *pycnocarpa* parent (furrowedness and lack of crinkledness of the leaves, green stem and all flower characters). This in a large measure, perhaps, accounts for patrocliny as a result of the reciprocal crosses. The segregate hybrid *tortuosa* inherits the greater number of its characters from the *nutans* parent (convexity and crinkledness of the leaves, red stem and all flower characters). The expectation was that reciprocal crosses between *nutans* and *tortuosa* would also result in patrocliny and this expectation was confirmed in the result. The results of all the back- and inter-crosses will not be described in detail, but are given in tables 2 to 9. The F_1 cultures of 1913-1914, and 1915, are combined in tables 2 and 3. The back- and inter-crosses listed in tables 4 to 9 were grown in 1915 unless otherwise indicated.

TABLE 2

F_1 generation of Oenothera nutans × Oe. pycnocarpa showing the splitting into the 4 hybrid types (1 = pycnocarpa; 2 = nutans).

2 × 1 (1913-1914) Total number plants F_1 = 118

	Nutella	*Pycnella*	*Tortuosa*	*Tortuella*
Annuals	35	10	0	0
Biennials	27	24	21	1
Total	62	34	21	1
2 × 1 (1915)	Total number plants F_1 = 154			
Annuals	140	10	2	2
Grand total	202	44	23	3 = 272

TABLE 3

F_1 generation of Oe. pycnocarpa × Oe. nutans, showing the splitting into 3 hybrid types. (1 = pycnocarpa; 2 = nutans.)

1 × 2 (1913-1914) Total number plants F_1 = 51

	Nutella	*Pycnella*	*Tortuosa*	*Tortuella*
Annuals	4	9	0	0
Biennials	2	36	0	0
Total	6	45	0	0
1 × 2 (1915)	Total number plants F_1 = 213			
Annuals	49	163	0	1
Grand total	55	208	0	1 = 264

TABLE 4

Back-crosses of hybrida nutella with the parents (1 = pycnocarpa, 2 = nutans).

74 = *Nutella* (2 × 1) × 2 =	*Nutans*	69		Total 122
	Pycnella	53		
75 = *Nutella* (1 × 2) × 2 =	*Nutans*			Total 128
58 = 2 × *Nutella* (2 × 1) =	*Nutella*	50	*8	Total 66
	Pycnella	2	6	
57 = 2 × *Nutella* (1 × 2) =	*Nutella*	90		Total 99
	Pycnella	8		
Mutant =	*Gracilis dwarf*	1		
73 = *Nutella* (2 × 1) × 1 =	*Pycnocarpa*	56	*22	Total 96
	Nutella	2		
Toothed stem leaves	*Tortuosa*	7	9	
52 = 1 × *Nutella* (2 × 1) =	*Nutella*			Total 118
51 = 1 × *Nutella* (1 × 2) =	*Nutella*	25		Total 26
	Tortuosa	1		

* The numbers in the second column of 58 and 73 were cultures of 1914.

TABLE 5

Back-crosses of hybrida pycnella with the parents (1 = pycnocarpa 2 = nutans).

61 = *Pycnella* (2 × 1) × 1 =	*Pycnocarpa*	156	Total 156
60 = *Pycnella* (1 × 2) × 1 =	*Pycnocarpa*	52	Total 52
53 = 1 × *Pycnella* (2 × 1) =	*Pycnella*	75	Total 75
(1914) 1 × *Pycnella* (1 × 2) =	*Pycnella*	25	Total 25
62 = *Pycnella* (2 × 1) × 2 =	*Nutella*	13	Total 106
	Pycnella	93	
(1914) *Pycnella* (1 × 2) × 2 =	*Nutella*	3	Total 21
	Pycnella	18	
54 = 2 × *Pycnella* (2 × 1) =	*Nutella*	90	Total 122
	Pycnella	6	
?	*Tortuosa*	26	
55 = 2 × *Pycnella* (1 × 2) =	*Nutella*	20	Total 21
	Pycnella	1	

TABLE 6

Back-crosses of hybrida tortuosa with the parents (1 = pycnocarpa, 2 = nutans).

68 = *Tortuosa* (2 × 1) × 2 =	*Nutans*	108	Total 108
56 = 2 × *Tortuosa* (2 × 1) =	*Tortuosa*	23	Total 25
	Tortuella	2	
67 = *Tortuosa* (2 × 1) × 1 =	*Nutella*	28	Total 29
or	*Pycnocarpa*	1	
	Pycnella		
50 = 1 × *Tortuosa* (2 × 1) =	*Nutella*	63	Total 148
	Pycnella	85	

TABLE 7

Inter-crosses of hybrida nutella and hybrida tortuosa (1 = pycnocarpa, 2 = nutans).

76 = *Nutella* (2 × 1) × *Tortuosa* (2 × 1) =	*Tortuosa*	17	Total 63
	Pycnocarpa	46	
72 = *Nutella* (1 × 2) × *Tortuosa* (2 × 1) =	*Pycnocarpa* (Numbers too small)	5	Total 5
69 = *Tortuosa* (2 × 1) × *Nutella* (2 × 1) =	*Nutella*	120	Total 127
	Pycnocarpa	5	
	Nutans	2	
70 = *Tortuosa* (2 × 1) × *Nutella* (1 × 2) =	*Nutella*	10	Total 10

TABLE 8

Inter-crosses of hybrida nutella and hybrida pycnella (1 = pycnocarpa, 2 = nutans).

78 = *Nutella* (1 × 2) × *Pycnella* (2 × 1) =	*Pycnella*	90	Total 120
	Nutans	29	
	Nutella	1	
65 = *Pycnella* (2 × 1) × *Nutella* (2 × 1) =	*Nutella*	18	Total 18
(1914) — *Pycnella* (1 × 2) × *Nutella* (2 × 1) =	*Nutella*	34	Total 34

TABLE 9

Inter-crosses of hybrida tortuosa and hybrida pycnella (1 = pycnocarpa, 2 = nutans).

72 = *Tortuosa* (2 × 1) × *Pycnella* (1 × 2) = *Tortuosa* ? or	*Nutella*	23	Total 39
	Nutans	16	
71 = *Tortuosa* (2 × 1) × *Pycnella* (2 × 1) = *Tortuosa or*	*Nutella*	62	Total 105
	Nutans	43	
64 = *Pycnella* (2 × 1) × *Tortuosa* (2 × 1) =	*Nutella*	54	Total 112
	Pycnocarpa	58	
63 = *Pycnella* (1 × 2) × *Tortuosa* (2 × 1) = *Tortuosa* ? or	*Nutella*	83	Total 112
	Pycnocarpa	25	
	Nutans	3	
	Tortuella	1	

This result is remarkable in that in the F_1 generation from a cross between two feral, non-mutating species, quadruple hybrids appear in the F_1 generation; one is a blend and self-sterile, but its pollen and egg cells are fertile; two of the selectives are fixed types and breed true, while the fourth hybrid (also selective) breaks up into different types in the second generation. The back- and inter-crosses show, either striking examples of patrocliny, or splitting into two types in some cases, three types in other cases and four types in one case.

In the back-crosses there are 9 cases of patrocliny, but probably only 5 of these are real (numbers 53, 60, 61, 62, 68). The other cases would probably show splitting if the numbers were larger (52, 70, 72, 75). But the position of the parents in the formula for No. 75, on the principle of an iterative cross (see DEVRIES, 1913, p. 94) may influence the predominance of *nutans* in the cross *nutella* (1 × 2) × 2 = *nutans*. In the formula in Nos. 60 and 68 the dominance of the extremes is in accordance with the expectation in double reciprocal crosses of DEVRIES, and so, in No. 61 for the expectation of the iterative cross. In other cases, however, the result, even where patrocliny is present, is not in accordance with the laws discovered by DEVRIES. This is in great part due to the fact that the F_1 splitting into several distinct types occurs on both sides of the reciprocal crosses, rather than patrocliny.

In the back-crosses there are at least 5 cases of patrocliny, 10 cases of splitting into 2 types, and 4 cases of splitting into 3 types. In the inter-crosses there are 2 cases of patrocliny, 3 cases of splitting into 2 types, 1 of splitting into 3 types, and 1 of splitting into 4 types.

But in all of the back- and inter-crosses no new types (with a single exception) appear, they all conform to one or other of the six types, the primary parental types, or one or more of the four F_1 hybrid types. The single exception is a mutant of the dwarf *gracilis* type.

THE BEHAVIOR OF *OENOTHERA NUTANS* AND *OE. PYCNOCARPA* COMPARED WITH OTHER WILD SPECIES OF OENOTHERA

DEVRIES (1913, pp. 30-59) has shown that the production of but one form of hybrid in the first generation of a cross between old, or wild species of Oenothera (section Onagra) is the general rule. But the hybrids from reciprocal crosses are often different in type (DEVRIES, 1903, p. 471; 1913, p. 30). The hybrids in these reciprocal crosses often resemble the pollen parent strongly, i. e., they are strongly patroclinous (*Oe. biennis* × *muricata*, etc.). The parents of such crosses he terms *heterogamous* species. A few of the wild species he has shown to be *isogamous*, i.e., the single hybrids of reciprocal crosses are identical (*Oe. Hookeri, Cockerelli* and *strigosa*, see DEVRIES, 1913, p. 59). The behavior of *Oe. nutans* and *pycnocarpa* in reciprocal crosses does not conform to either of the types of behavior found by DEVRIES to be characteristic of the heterogamous or isogamous species which he has studied. So far as the vegetative characters are concerned patrocliny can not be ascribed to either of the hybrids, for the characters are either blended (in *hybrida nutella*) or selected and distributed about equally from the parents to two of the selective hybrids (*pycnella* and *tortuosa*).

In the selectives, while certain characters resemble those of one parent, other characters resemble those of the other parent and it is difficult to say which set of characters dominates. But even if one hybrid should be judged to indicate patrocliny in one cross, the same hybrid appears in the reciprocal cross where it would be a case of matrocliny for the same hybrid. While the behavior of *pycnocarpa* and *nutans* in reciprocal crosses is similar to that of isogamous species, in that the hybrid production in one cross is the same in the reciprocal cross,[11] there are three to four different hybrids instead of one, as in the wild isogamous species like *Oe. Hookeri, Cockerelli* and *strigosa*. Nevertheless, since the same types of hybrids are produced on each side in reciprocal crosses, it seems to indicate that the same heritable characters are transmitted in the pollen and egg cells. In this respect the parents (*pycnocarpa* and *nutans*) behave like isogamous species, but differ from such isogamous species as *Oe. Hookeri, Cockerelli* and *strigosa* in the production of several distinct

[11] Only 3 hybrid types have thus far appeared in the cross *Oe. pycnocarpa* × *nutans*.

hybrid types, all of which, in their vegetative characters are blends or recombinations of the parental characteristics.

INTERPRETATIONS OF SPLITTING IN THE FIRST GENERATION

Selection of characters in the zygote versus Mendelian segregation

The selection and blending of the factors which make up the constitution of the two parents (*nutans* and *pycnocarpa*), into the three selective hybrids (*pycnella, tortuosa,* and *tortuella,* and the blend hybrid (*nutella*), occurs in the zygote or fertilized egg. Therefore it is of a very different type from that which takes place in Mendelian segregation. No such qualitative division as occurs in the gonotokonts, providing for the segregation of factors in Mendelian hybrids, is known to take place in the fertilized egg, and can not be invoked to explain zygotic selection.

Very little is known of the cytological processes in the fertilized egg of plants, so far as it relates to the more critical stages in the organization of the nuclear figure for the first division, and the behavior of the paternal and maternal chromosomes in the organization of a working relation in the new diploid nucleus. GUIGNARD (1890) describes and figures the spindle for the first division of the fertilized egg in *Lilium Martagon.* It is preceded by a double gnarl stage representing the paternal and maternal nuclear chromatin skeins. But the formation and association of the paternal and maternal chromosomes in the zygote was not observed. In *Pinus Strobus* MARGARET C. FERGUSON (1901, 1904) has shown that while the sperm and egg nuclei are in close contact the spindle is organized between them, while the paternal and maternal chromosomes form from the chromatin net-work of the sperm and egg respectively and move to the nuclear plate of the spindle. In two successive divisions the paternal and maternal chromosomes are formed in separate groups. But their final arrangement and relation, as cell wall formation and the morphogenic processes begin in the embryo, were not determined. STRASBURGER (1904, p. 20) attempted to study the relation of the paternal and maternal chromosomes in the fertilized egg of Funkia and Galtonia, where the chromosomes are of different sizes, but was unable to accomplish the desired result because of the rarity of seed formation. In the fertilized egg of *Iris Siberica* and *Triticum vulgare,* he discovered nothing unusual. The difficulties met with in the study of the cytological processes of the first division of the fertilized egg in plants appear to be very great. But it is an important and critical stage in the life cycle of plants, which deserves investigation.

Is the production of these quadruple hybrids due to the mutating condition of one of the parents?

The appearance of quadruple hybrids in the F_1 generation of a cross between two wild, non-mutating species is a rather unique phenomenon. Twin hybrids regularly appear in crosses of *Oe. Lamarckiana* or certain of its derivatives, with certain wild, non-mutating species of Oenothera, as demonstrated by DEVRIES (1907, 1909, 1913). These crosses are termed by DEVRIES *"mutation crosses."* Triple and even quadruple hybrids appear in certain mutation crosses. But heretofore triplets or quadruplets in the F_1 generation have only appeared when the mutant parent is an inconstant race and tends to repeat itself in crosses.

Oenothera nutans and *Oe. pycnocarpa* are constant, non-mutating feral species. The progeny is remarkably uniform, has been grown in several successive generations, presents a high degree of seed and pollen fertility, breeds true and the gametes are uniform. The two species have appeared each year, in typical form, in the same locality where they were discovered in 1909.

The number of plants grown in successive generations is shown in the following table.

TABLE 10

	Nutans	*Pycnocarpa*
1911-12	100	50
1913-14	75	198
1915-	152	76
1916	15	20

In 1916 very few of the seedlings grown in the pans were transplanted to the garden, since only a few plants were desired to raise seed and for a few pollination experiments. Each year the percentage of seed germination was high though the actual percentage was not determined by counting. The seeds were sown in good potting-room soil in seed pans 4-6 inches in diameter. The seeds were then covered with a rather thick layer of pure sand or fine gravel, so that the cover would not cake. Gravel and coal ashes are favorite substrata for oenotheras. The soil was kept well watered and a favorable temperature was maintained. Where an abundance of seed was sown, large numbers of seedlings developed so that in most cases they were closely packed in the pans. In such cases not all of the seedlings were transplanted to the garden, but great care was taken to select from among all sizes of seedlings in the

pan, in order to be certain that different types were not represented by the smaller and younger seedlings. The evidence therefore is very strong that *Oenothera nutans* and *Oe. pycnocarpa* in cultures are pure lines, notwithstanding the unwarranted assumption by DAVIS (1916, p. 245) that they are of "doubtful genetic purity."

This assumption appears to be based on the very questionable hypothesis that, since twin, triple or quadruple hybrids appear in the F_1 generation of a cross, one or both of the parents are mutating species and that a mutating species is *per se* genotypically impure.[12] Numerous cases are known in pure line work, where mutations have arisen from a pure line. N. H. NILSSON of the Swedish Experiment Station at Svalöf has described a mutant with stiff straw and stout heads from a pure line of wheat (see JOHANSSEN 1909, p. 443). According to DEVRIES (1907 b, p. 85) the workers at "Svalöf are satisfied that real mutations as well as accidental crosses are occurring in their pure pedigree-cultures, from time to time." JOHANSSEN (1909, p. 457) relates the appearance of a mutation from one of his pure lines of beans. He also cites other cases of mutations from pure lines in animals as well as in plants. The evidence of their appearance in pure lines is abundant.

No mutations in the pure lines of *Oenothera nutans* and *Oe. pycnocarpa* have appeared, though several mutants have been thrown in my cultures of *Oenothera Lamarckiana* where the number of individuals in the culture varied from 75 to 100. Among all the crosses (parental, back- or inter-crosses) only one mutant has appeared in the hybrid progeny of *nutans* and *pycnocarpa*. This was a *gracilis* dwarf mutant in the back-cross *nutans* × *nutella* (1 × 2).[13] But the appearance of a mutant is not an indication that the line is impure, and furthermore this mutant did not appear in the direct line of either parent, but in one of the back-crosses.

The appearance of triple and quadruple hybrids in the F_1 generation of reciprocal crosses between *Oe. nutans* and *Oe. pycnocarpa* can not be explained on the basis of the interesting theory of "mutation crosses" in the same sense as interpreted by DEVRIES. We have no evidence that the species are mutating, and furthermore the four hybrids of the F_1 generation are very different from the twin hybrids of DEVRIES's mutation crosses. In mutation crosses, according to DEVRIES, there is a splitting of the entire constitution (gametic) so that all the vegetative char-

[12] JOHANSSEN says (1909, p. 448) that the oft repeated conjecture that mutations indicate the hybrid nature of the parent has little worth.

[13] See table 4.

acters are split, not selected as in *pycnella, tortuosa* and *tortuella,* nor equally blended as in *nutella.*

The four different hybrid types in the F_1 generation of crosses between *Oe. pycnocarpa* and *Oe. nutans* differ from the mutation crosses described by DEVRIES in another respect. In the mutation crosses triplets and quadruplets are formed only when the mutant parent is an inconstant race, for example, *Oe. lata,* which is nearly pure female, though rarely *lata*-like forms which produce pollen appear in the F_1 when *lata* is crossed with other species (DEVRIES 1913, p. 245). When *Oe. lata* is pollinated with *Oe. Hookeri, Cockerelli, biennis Chicago,* etc., the splitting in the first generation produces the twins, *laeta* and *velutina,* and in addition a third form which is *lata* repeated, but slightly modified. The most common modified form of this *lata* arising by splitting in the first generation of a cross shows a resemblance to *laeta* forms and is called *lata-laeta.* Besides the splitting in the F_1 generation into twins, *laeta* and *velutina,* the inconstant race repeats itself. The repeated form is modified by *laeta* characters (the "triplet") and rarely a small percentage is modified by the *velutina* characters ("quadruplet"). This is strong additional evidence that the triple and quadruple hybrids in the first generation of crosses between the wild species *Oe. pycnocarpa* and *Oe. nutans,* represent a type of splitting different from that manifested in the mutation crosses of DEVRIES, and does not appear capable of interpretation on the same hypothesis.

The three hybrids, *pycnella, tortuosa* and *tortuella,* have been spoken of as selective hybrids, since certain parental factors are selected in the zygote, and the characters they represent are developed to their full expression, other factors being either eliminated or subordinated, so that they do not enter into the composition, at least the phenotypic composition, of the new types. If they were true segregates in their genotypic constitution, the interesting question would arise as to how this segregation of certain factors in the zygote, and the elimination or subordination of others, takes place. In Mendelian segregation the mechanism of allotypic division in the gonotokonts is generally accepted as furnishing a means for the segregation. But no such mechanism of nuclear divisions occurs in the zygote. The stage of fecundation and the first nuclear division in the zygote is a critical period in the ontogeny of the individual, and particularly so in the F_1 zygote of crosses.

If there is an elimination of certain factors in the composition of these selective hybrids, we may conceive that it takes place by the shunting to one side, during nuclear division in the zygote, of some of the factor-

bearing material, a phenomenon, perhaps, similar to merogony as recently defined by GOLDSCHMIDT (1916). GOLDSCHMIDT (1912) sought to find a cytological basis for patrocliny exemplified in DEVRIES'S crosses of *Oenothera biennis* and *Oe. muricata,* etc., where the F_1 hybrid in its vegetative characters is nearly or quite identical with the pollen parent. His first cytological interpretation of this phenomenon predicated the degeneration of the egg cell, there being no fusion of the sperm and egg, so that the embryo was developed exclusively from the male cell. According to his recent studies on material of reciprocal crosses of *Oe. atrovirens* and *Oe. venosa* there is a fusion of the sperm and egg cells, but during the first division of the zygote the chromosomes from the egg are eliminated from the daughter nucleus of the embryo cell and degenerate in the cytoplasm. Such a process, if the hereditary factors are carried by the chromosomes alone, would result in the complete reproduction of the pollen parent in the F_1, not modified by the ovule parent. But in cases of patrocliny among the Oenotheras, where the flower and inflorescence characters are different in the two parents, the F_1 plants, while very strongly resembling the pollen parent in vegetative characters, often resemble the ovule parent more or less strongly in the inflorescence.

The fact that the patroclinous F_1 generation in such Oenothera crosses is more or less modified by the maternal characteristics, especially in the inflorescence, indicates that factor-bearing material is contributed to the F_1 generation by the mother plant of the cross. It should be said, however, that GOLDSCHMIDT (1912) does not commit himself unreservedly to the merogony theory as an explanation of patrocliny in the Oenotheras. It appears to me that these cases of patrocliny in the Oenotheras, where the hybrid is fixed in the F_1 generation, are examples of *permanent dominance,* such hybrids being *physiological homozygotes.*

Stable and unstable dominance in the hybrids pycnella, tortuosa and tortuella

I have sometimes spoken of these hybrids as "segregate" hybrids, because they at least appear to be segregates in their phenotypic constitution. But I have been led to believe from a study of my Oenothera cultures during the past two seasons, that these three hybrids can be classed as cases of selective dominance, though perhaps not in the strict Mendelian sense. If there were a splitting in the F_2 generation, releasing the parent forms in 50 percent of the progeny and forming 50 percent heterozygotes there would be no question that *hybrida pycnella* and *hybrida tortuosa* in the F_1 generation were true Mendelian dominants, for the F_1 hybrids in Mendelian crosses are often intermediates. In each of

these hybrids dominance of parental characters is complete in relation to nearly all the visible characters. But not all of the dominant characters of either hybrid come from a single parent. There is a selection of factors from each parent, a "crossing over" between the linked factors. A certain group of factors is dominant in *pycnella,* while another group of factors is subordinate. The group of subordinate factors in *pycnella* becomes the dominant one in *tortuosa.* Since these *hybrids* are fixed in the F_1 generation they may be considered as cases of fixed or permanent dominance.[14] They are physiological homozygotes.

In support of this interpretation of the genotypic constitution of *pycnella* and *tortuosa* is the fact that in certain of the back-crosses where splitting occurs in the zygote, *nutella* is one of the "segregates." In these back-crosses *nutella* is not one of the parents. This behavior is shown in the following tables; compiled from tables 5 and 6.

TABLE 11

Back-crosses of hybrida pycnella with parent nutans (2 = nutans, 1 = pycnocarpa).

62 = *Pycnella* (2 × 1) × 2 =	*Nutella*	13	Total	106
	Pycnella	93		
(1914) *Pycnella* (1 × 2) × 2 =	*Nutella*	3	Total	21
	Pycnella	18		
54 = 2 × *Pycnella* (2 × 1) =	*Nutella*	90	Total	122
	Pycnella	6		
?	*Tortuosa*	26		
55 = 2 × *Pycnella* (1 × 2) =	*Nutella*	20	Total	21
	Pycnella	1		

TABLE 12

Back-crosses of hybrida tortuosa with parent pycnocarpa (2 = nutans, 1 = pycnocarpa).

67 = *Tortuosa* (2 × 1) × 1 =	*Nutella*	28	Total	29
	Pycnocarpa	1		
	Pycnella			
50 = 1 × *Tortuosa* (2 × 1) =	*Nutella*	63	Total	148
	Pycnella	85		

[14] The term *permanent,* or *stable, dominance,* relates to the fixity of the type in the F_1 generation of a cross so that if selfed, the type appears in successive generations unchanged. It implies also the permanent recessiveness, latency or subordination of the other factors in the F_1 zygote of the cross which were not activated. In *unstable dominance,* the type appearing in the F_1 generation is not fixed, but splits or shows extraordinary fluctuation in the F_2. *Selective dominance* relates to the dominance of the active factors in a selective hybrid.

In table 11 it is seen that from the back-crosses of *hybrida pycnella* with parent *nutans*, 270 in all, there appear 126 individuals of *hybrida nutella*. Parent *nutans* and *hybrida pycnella* it will be remembered, both have broad rosette leaves somewhat toothed over the basal portion. The rosette leaves of *hybrida nutella* are intermediate in width and edge character between the broad and toothed leaves of parent *nutans* and the narrow cut leaves of parent *pycnocarpa*. The factor for this character (narrowness and cutness of rosette leaves, and some others also) of *pycnocarpa* must, therefore, be present in *hybrida pycnella* of these back-crosses, but in a latent or "recessive" state. When *hybrida pycnella* is back-crossed with parent *nutans* these latent factors become active in a large percent of the zygotes and the blend *hybrida nutella* appears.

In like manner, as seen from table 12, in the back-crosses of *hybrida tortuosa* with parent *pycnocarpa*, 177 in all, there appear 91 individuals of the blend, *hybrida nutella*. Since both *tortuosa* and *pycnocarpa* have narrow, cut leaves, the factor for width and edge character of the rosette leaves of parent *nutans* (other factors also) must be present in *tortuosa*, but in a subordinate, or "recessive" state.

These back-crosses, therefore, present evidence that in each of the hybrids, *pycnella* and *tortuosa*, certain factors, selected some from one parent, some from the other, are active or dominant[15] in the zygote of the F_1 and the characters they represent are developed to their full expression. The alternative factors are subordinate or "recessive" in each hybrid and become active in a certain percentage of the zygotes of back-crosses. The result of this analysis of the hybrids indicates quite clearly that the gametes of *Oenothera nutans* and *Oe. pycnocarpa* are uniform. It is not necessary to resort to the rather overworked hypotheses of dissimilar gametes in the parents of twin hybrids, nor of those giving a larger number of distinct hybrids in the F_1 generation, except where one of the parents is an inconstant race, as in *Oenothera lata*, etc. The evidence from Oenothera cultures points more and more to the conclusion of SHULL (1914) that "a hereditary mechanism must exist in Oenothera fundamentably different from that which distributes the Mendelian unit-characters."

[15] SWINGLE (1898, 1913) has proposed a hypothesis for the different types of hybrids appearing in the first generation of interspecific crosses which he calls "zygotaxis." It assumes the chance arrangement of the parental chromosomes in different positions in different zygotes. These positions are maintained throughout the ontogeny. Those chromosomes situated nearer the cytoplasm are better fed and exercise a greater influence on the formative processes in the cell than those more distant. In consequence of the different arrangement in different zygotes, different hybrid types appear.

In *tortuella*, which differs from *tortuosa* in having a green stem instead of a red one, the dominance of the factor composition in the F_1 is not fixed. A breaking-down takes place in the F_2 generation. The complete composition of the individuals of this second generation can not be determined until they come into flower in 1917; but from the types of rosette present it is clear that in *tortuella* certain factors are present in its genetic constitution which are subordinated in the F_1 and only come into play in some of the individuals of the F_2 (breadth and edge character of the rosette leaves for example).

We do not know the behavior of *hybrida nutella* in the F_2 generation, and cannot say whether or not it is a physiological homozygote. It is almost a perfect blend of the two parents. Besides certain features of the inflorescence and fruit spike which differ to some extent from each parent and do not represent an intermediate condition, the petals are more like those of *nutans*, and it might be considered a dominant in the F_1 favoring *nutans*.

Multiple dominance[16] *in the F_1 generation of crosses between Oenothera nutans and Oe. pycnocarpa*

On this interpretation, then, there are four types of dominance in the F_1 of crosses between *Oe. nutans* and *pycnocarpa*. All four appear when *pycnocarpa* is the pollen parent. Only three have thus far appeared when *nutans* is the pollen parent. Two of these, *pycnella* and *tortuosa* are fixed dominants, and are physiologically homozygous. The genotypic constitution of the F_1 dominant *tortuella* is dissolved in the F_2. The later history of *nutella* is unknown.

In many cases interspecific crosses are difficult or impossible to obtain. In general this difficulty is greater in proportion to the remoteness of the relationship between the species used in the attempted cross. There is apparently great difficulty in establishing a working relation between the sperm and egg nuclei after their association, whether of a chemical or mechanical nature. The disturbance caused by the entrance of a foreign sperm into the egg should not be overlooked. Chemical, enzymatic and mechanical disturbances result, the effect of which may vary according to the differences in the constitution of the parents used in the cross. The reciprocal shock on the germ cells when they meet in the egg may be sufficient in many cases to break some of the remoter

[16] Multiple dominance relates to the appearance of several distinct hybrid types in the F_1 of a cross, certain factors being completely or partially dominant in each type, the other factors being subordinate, latent, or recessive.

linkages of factors in the parents. Chance then partly determines the new association in the four different hybrid types in the F_1 of *Oe. nutans* × *pycnocarpa*.[17]

All, or nearly all, the active factors of the two parents enter equally active and with the same association, into the constitution of the zygote of the blend, *hybrida nutella*. The effect of the shock merely retards somewhat the organization of a working relation between the sperm and egg nuclei.

In the three other hybrids the effect of the shock is such, that, when the organization of a working relation between the germ cells is formed, certain factors are rendered subordinate or inactive. The shock, to use a figurative expression, shakes up the elements of the composition, "crossing over" occurs, and they fall into new combinations, or alliances, or systems. To some extent chance probably determines the new combinations but there are varying degrees of linkage between certain factors. Among the factors relating to the leaves, linkage is strong in couplets, as width and edge character, convexity and crinkledness, furrowedness and lack of crinkledness. In the case of the flowers the linkage among all the factors of each parent is strong. While the shock breaks the general bond of linkage of the sum total of factors in each species, it does not destroy the linkage present in lesser associations of factors. To some extent chance determines whether one or the other of the "selective" hybrids is formed. In two of these hybrids (*pycnella* and *tortuosa*) the activity or inactivity of the factors is fixed so long as the hybrids are self-fertilized. They breed true in the F_2 and following generations, since they are physiologically homozygous. But patrocliny and splitting occurs in the back- or inter-crosses. In *hybrida tortuella*, when the working relation is established between the factors of the germ cells in the F_1 zygote, the activity or inactivity of certain factors is fixed only for the F_1 generation. The organization of the working relation between the factors is unstable, and breaks down in the second generation into, perhaps, numerous types, as in certain other species hybrids (see BAUR 1911, p. 207). Since some of the types presented in this F_2 generation have the breadth and edge character of the leaves of the parent *nutans*, a character not present in the phenotype of *hybrida tortuella*, its appearance in the F_2 generation of *tortuella* indicates that the *nutans* factor for breadth and toothedness of the rosette leaves was present in *tortuella* but in a subordi-

[17] The result would vary in different species crosses according to the firmness with which the association of factors in either parent held to its genotypic type.

nate condition. In the fixed "selective" hybrids the color of the stem is linked with flower characters in the same way as in the parents.

In *hybrida pycnella* greenness of stem is linked with *pycnocarpa* flowers, in *hybrida tortuosa* redness of the stem is linked with *nutans* flowers. In *hybrida tortuella* this link between color of the stem and flower characters is broken. It is possible that this may be evidence present in the first generation that many of the linkages among factors in the parents are broken, thus rendering the composition of *tortuella* very unstable. This splitting of *hybrida tortuella* in the second generation does not appear to be of the Mendelian type.

One cause of the peculiar behavior of the Oenotheras may be that the association, or linkage of factors, is not very strong in the germ plasm, but varies in that respect in different species. The germ plasm is peculiarly sensitive to shock from the meeting of sperm and egg, particularly when there is a genotypic difference between the two germ plasms. This results more or less in interchange, crossing over, dominance, as well as blending, of factors in the zygote, often accompanied by selection of factors into different associations in different zygotes giving rise to more than one hybrid type in the F_1 generation of crosses.

SUMMARY

1. In the F_1 generation of the cross *Oenothera nutans* × *Oe. pycnocarpa,* four different hybrid types appear which are named as follows: *Oe. hybrida nutella; Oe. hybrida pycnella; Oe. hybrida tortuosa;* and *Oe. hybrida tortuella.* In the F_1 generation of the reciprocal cross, *Oe. pycnocarpa* × *Oe. nutans* three hybrid types have appeared which are identical with three of the types named, viz., *nutella, pycnella* and *tortuosa.* If the number of the individuals of the F_1 *pycnocarpa* × *nutans* was very large it is probable that *tortuella* also would appear.

2. *Nutella* is a *blend* hybrid; all the homologous factors of the parents are active and the phenotype is a mean between the two parents, with some exceptions in the inflorescence. Thus far *nutella* has proven absolutely self-sterile, but the pollen and egg cells are highly fertile in back- and inter-crosses, and in reciprocal crosses with other species.

3. *Pycnella* and *tortuosa* are *selective* hybrids. For example, in the F_1 zygote which develops into *pycnella,* all of the factors of the two parents are present. Certain of these factors from each parent are selected in the organization of the working relation between them, and the characters they represent are developed to their full expression, while the other members of the homologous factors remain subordinate.

Tortuosa is organized in a similar way, but the factors which are subordinate in *pycnella* are active in *tortuosa*, and *vice versa*. In phenotypic constitution *tortuosa* and *pycnella* are counterparts of each other.

4. *Pycnella* and *tortuosa* are physiological homozygotes; they are fixed in the first generation, and when selfed they are repeated in the F_2 and succeeding generations.

5. *Tortuella* is also a selective hybrid, but it is not fixed in the F_1; when selfed it dissolves in the F_2 into numerous types, some of which show that certain factors which were subordinate in the F_1 are activated in the F_2.

6. The production of 4 hybrid types in the F_1 is an example of multiple dominance i.e., many dominant types appear. *Pycnella* and *tortuosa* are examples of permanent or stable dominance of factors.

7. In back-crosses there are clearly 5 cases of patrocliny, 10 cases of splitting into 2 types, and four cases of splitting into 3 types.

8. In the inter-crosses there are 2 cases of patrocliny, 3 cases of splitting into 2 types, 1 of splitting into 3 types, and 1 of splitting into 4 types.

9. In all of the back- and inter-crosses no new types (except a dwarf *gracilis*) appear; they all conform to one or other of the six types, the primary parental types, or one or more of the four F_1 hybrid types.

10. In the back-crosses of the selective hybrid *pycnella* with parent *nutans*, and of the selective hybrid *tortuosa* with parent *pycnocarpa*, the blend hybrid *nutella* appears in a high percentage of the progeny. A number of the phenotypic characters of parent *pycnocarpa* are not present in the phenotype of *pycnella*. The factors for these characters, however, must be subordinate or latent in *pycnella* for when crossed with parent *nutans* these subordinate *pycnocarpa* characters are activated in a high percentage of cases and make possible the appearance of the blend *nutella*. Likewise in back-crosses of *tortuosa* and *pycnocarpa*, the subordinate *nutans* factors in *tortuosa* are activated in a high percentage of cases and make possible the appearance of the blend hybrid *nutella*.

11. The analysis summarized in Nos. 5 and 10 indicates that the gametes in the parents *nutans* and *pycnocarpa* are uniform.

LITERATURE CITED

ATKINSON, GEO. F., 1913 Is the biennial habit of Oenothera races constant in their native localities? Science N. S. **37**: 716, 717.

1914 Segregation of characters in first generation hybrids from stable species of Oenothera. Science N. S. **39**: 256 (idem., pp. 3, 4, in separate for Bot. Soc. Am.)

1914 Segregation of "unit characters" in the zygote of Oenothera with twin and triplet hybrids in the first generation. Science N. S. **39**: 834, 835.

1916 The F_2 generations, and back- and inter-crosses of the F_1 hybrids between *Oenothera nutans* and *pycnocarpa*. Science N. S. **43**: 720.

BARTLETT, H. H., 1911 Systematic studies on Oenothera. I. *Oenothera Tracyi*, sp. nov. Rhodora **13**: 209-211, pl. 93.

1913 Systematic studies on Oenothera, II. The delimitation of *Oenothera biennis*. Rhodora **15**: 48-53; III. New species from Ithaca, N. Y. Rhodora **15**: 81-85.

BAUR, E., 1911 Einführung in die experimentelle Vererbungslehre. 293 pp. Berlin: Gebr. Borntraeger.

BLARINGHEM, L., 1913 Sur l'hérédité en mosaic. IVe Conférence internationale de génétique (Paris 1911), pp. 101-131, text figs. 1-18.

CANNON, W. A., 1903 Studies in plant hybrids: The spermatogenesis of hybrid cotton. Bull. Torr. Bot. Club **30**: 133-172, pls. 7, 8.

DAVIS, B. M., 1910 Genetical studies on Oenothera I. Notes on the behavior of certain hybrids of Oenothera in the first generation. Am. Nat. **44**: 108-115.

1916 Hybrids of *Oenothera biennis* and *Oenothera Franciscana* in the first and second generations. Genetics **1**: 197-251, figs. 1-26.

1916 *Oenothera neo-Lamarckiana*, hybrid of *Oe. Franciscana* Bartlett × *Oe biennis* Linnaeus. Am. Nat. **50**: 688-696.

EAST, E. M., 1915 The phenomenon of self-sterility. Am. Nat. **49**: 77-87.

FERGUSON, MARGARET C., 1901 The development of the egg and fertilization in *Pinus Strobus*. Ann. Bot. **15**: 435-479, pls. 23-25.

1904 Contributions to the knowledge of the life history of Pinus with special reference to sporogenesis, the development of the gametophytes and fertilization. Proc. Washington Acad. Sci. **6**: 1-202, pls. 1-24.

FOCKE, W. O., 1881 Die Pflanzen-Mischlinge, ein Beitrag zur Biologie der Gewächse. 569 pp. Berlin: Gebr. Borntraeger.

GATES, R. R., 1913 A new Oenothera. Bull. Torr. Bot. Club. **15**: 45-48, pls. 100, 101.

GATES, R. R., and THOMAS, N., 1914 A cytological study of *Oenothera* mut. *lata* and *Oe.* mut. *semilata* in relation to mutation. Quar. Jour. Micr. Sci. **59**: 523-571, text figs. 1-4.

GOLDSCHMIDT, R., 1912 Die Merogonie der Oenotherabastarde und die doppeltreziproken Bastarde von de Vries. Arch. Zellf. **9**: 331-344.

1916 Nochmals über die Merogonie der Oenotherabastarde. Genetics **1**: 348-353, pl. 4.

GUIGNARD, L., 1890 Études sur les phenomènes morphologiques de la fécondation. Bull. Soc. Bot. France **36**: C-CXLVI, pls. 3-5, (1889).

JOHANSSEN, W., 1909 Elemente der exakten Erblichkeitslehre. vi + 516 pp. Jena: Gustav Fischer.

JUEL, H. O., 1900 Beiträge zur Kenntniss der Tetradentheilung. Jahrb. f. wiss. Bot. **35**: 626-659, pls. 15, 16.

METCALF, H., 1901 Proc. Nebraska Acad. Sci. **7**: 109, 1901.

ROSENBERG, O., 1903 Das Verhalten der Chromosomen in einer hybriden Pflanze. Ber. d. deutsch. bot. Ges. **21**: 111-117, pl. 7.

1904 Über die Tetradenteilung eines Drosera-Bastardes. Ber. d. deutsch. bot. Ges. **22**: 47-51, pl. 4.

1909 Cytologische und morphologische Studien an *Drosera longifolia* × *rotundifolia*. Kungl. Sven. Vet. Akad. Handl. **43**: 1-64, figs. 1-33, pls. 1-4.

SHULL, G. H., 1914 A peculiar negative correlation in Oenothera hybrids. Jour. Genetics **4**: 83-102.

STRASBURGER, E., 1904 Über Reduktionsteilung. Sitzungsb. Akad. Wiss. Berlin, pp. 587-615, text figs. 1-9.

1904 Histologische Beiträge zur Vererbungsfrage I. Typische und allotypische Kernteilung. Jahrb. f. wiss. Bot. **42**: 1-71, pl. 1.

1908 Chromosomenzahlen, Plasmastrukturen, Vererbungsträger und Reduktionsteilung. Jahrb. f. wiss. Bot. **45**: 479-570, pls. 1-3.

1909 Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und Reduktionsteilung. Hist. Beitr. **7**: xvi + 1-123, pls. 1-3.

SWINGLE, W. T., 1898 Some theories of heredity and the origin of species considered in relation to the phenomena of hybridization. Bot. Gaz. **25**: 111-113.

1913 Variation in first generation hybrids (imperfect dominance): its possible explanation through zygotaxis. IV^e^ Conférence internationale de génétique. Paris 1911. Pp. 381-394, text figs. 1-10.

DEVRIES, H., 1903 Die Mutationstheorie, Vol. **2**, xvi + 752 pp. Leipzig: Veit & Co.

1907 a Twin hybrids. Bot. Gaz. **44**: 401-407.

1907 b Plant breeding; Comments on the experiments of NILSSON and BURBANK. xiv + 360 pp. Chicago: Open Court Pub. Co.

1908 Über die Zwillingsbastarde von *Oenothera nanella*. Ber. d. deutsch. bot. Ges. **26A**: 667-676.

1909 On triple hybrids. Bot. Gaz. **47**: 1-8.

1911 Über doppeltreziproke Bastarde von *Oenothera biennis* L. und *Oe. muricata* L. Biol. Centralbl. **31**: 97-104.

1913 Gruppenweise Artbildung, unter spezieller Berücksichtigung der Gattung Oenothera. viii + 365 pp. Berlin: Gebr. Borntraeger.

INHERITANCE OF A MOSAIC PERICARP PATTERN COLOR OF MAIZE[1]

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	261
Previous studies on variegation	261
The material used and method of attack	264
Continuous selection for type	265
Results of selection experiments	271
Crosses between selected types	271
Results of crossing homozygous types	276
Discussion and interpretation of results	278
SUMMARY	280
LITERATURE CITED	281

INTRODUCTION

Selection experiments for the purpose of testing JOHANNSEN's pure line hypothesis have given radically different results. In some cases selection within the pure line has served to isolate new types in which the character studied is progressively changed in the direction of the selection (JENNINGS 1916). In other experiments continued selection of plus and minus variates has not altered the mean of the progeny to any appreciable extent. This would indicate that some characters are in a much more stable condition than others. Mosaic or variegated pattern colors are examples of characters which exhibit a high degree of variability. For this reason carefully planned selection experiments with this class of characters should be of especial interest. The purpose of this paper is to describe experiments with a mosaic pericarp pattern color of maize.

PREVIOUS STUDIES ON VARIEGATION

DE VRIES (1910, pp. 113-160) carried on a number of experiments with variegated flowers. A brief summary of his work with *Antirrhinum*

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majus luteum striatum shows the general nature of his results. He found the variety *striatum* to be an inconstant race. There was found to be a continuous range of variation from narrow- to broad-striped forms. The narrowly striped forms gave only a small percentage of self red types (from 2 to 5). The broadly striped individuals gave a percentage of from 11 to 42 self red individuals. The self red form obtained from variegated parentage gave a progeny of about 25 percent variegated and 75 percent red. This variegated type is an example of an "eversporting variety." This term is applied to a race *"which produces in every generation a fairly constant proportion of atavists."*

CORRENS (1910) reported a study of the inheritance of the self green condition which appeared as a bud sport on variegated-leaved plants of Mirabilis. The green branches gave a progeny of about 75 percent green and 25 percent variegated. Of the 75 percent green plants approximately one-third bred true for self green and two-thirds again gave 75 percent green and 25 percent variegated.

EAST and HAYES (1911) report the case of an ear which was found in a field of dent maize of unknown parentage. This ear had seeds with a red pericarp on one side and seeds which were white or had a narrow red stripe on the other side. As no other red ears appeared in the field, it was supposed that this ear was nearly all pollinated by white. The red seeds gave a progeny of 50 percent red ears and 50 percent white ears. The white and striated seeds gave 50 percent ears with some striated seeds and 50 percent with white seeds. The result was explained on the basis that the plant due to produce a red ear varied somatically so that a part of the ear was red the other part white and striated.

EMERSON (1914) reports experiments with a recurring somatic variation in variegated ears of "Calico" dent corn, *Zea mays indentata*. The variegated condition is the result of stripes of red occurring on the pericarp of the seeds, the remaining area being colorless or showing a sort of washed out red. In some cases there were seeds with a colorless pericarp and also seeds with self red pericarp scattered over the same ear. Rarely, freak ears were found with a patch of self red or nearly self red grains. The number and width of the red stripes were very variable, the range of variation being from ears with only a single narrow stripe on one seed to ears with a few seeds striped, the remaining seeds having a self red pericarp.

Self-fertilized ears of this variegated race were obtained and seeds with various amounts of red were selected. The results showed that the more red there was in the seed planted the larger the percentage of red

ears in the progeny. The pollination of an uncolored race by the variegated race gave about 12 percent self red ears which showed that some of the male gametes of the variegated race carried factors for self red.

The red ears obtained from self-fertilized seed of homozygous variegated ears behaved as if they were F_1 crosses between red-eared and variegated-eared races, and gave a progeny with a ratio of approximately three self red ears to one variegated ear. In later generations a portion of the self red ears bred true.

EMERSON concludes that the fact that variegated plants occasionally produce self red ears is not in general to be taken as an indication that the variegated plants in question are heterozygous, but that such behavior seems to be inseparably associated with variegation. His results are explained on the hypothesis that in a homozygous race, one of the factors for variegation *V* changes to a factor for self color or *S*. No attempt is made to explain the cause of this change, although the author mentions the possibility that this is due to changing metabolic processes in the maturing plant, or to external influences, or to a quality inherent in the factor itself. EMERSON shows that the results of DE VRIES, CORRENS, and EAST and HAYES, can be explained in a similar manner.

The recent experiments by STOUT (1915) on selection of somatic variations show that variegated pattern colors of Coleus are very variable. He found that bud variations were common and the conclusion was reached that "in Coleus asexual and sexual reproduction were not fundamentally different in respect to the extent and range of variation." Sexual reproduction produced all types of variation in F_1, which shows that the characters dealt with were heterozygous. No evidence was found of the somatic segregation of invariable pattern factors. This was thought to be due to the fundamental relations between the chemical compounds involved.

On submitting this paper for publication the author learned that a further study with variegated pattern colors of dent maize had been made by EMERSON and would appear in an early number of GENETICS. These recent investigations (EMERSON 1917) were made by pollinating the progeny of variegated maize races by colorless strains. A careful separation of the seeds of the ears thus obtained was made. "Self-colored, partly self-colored, variously variegated and colorless seeds from variegated parent ears, thus pollinated, have given progenies containing a percentage of self-colored ears roughly proportional to the amount of self color in the seeds planted."

Evidence is given for two, and possibly more, distinctly different types

of variegation. The two types which were clearly demonstrated were called very light variegated and medium variegated. The very light variegated type, V_lV_l, "has little red (or brown) color—few more or less fully self-colored seeds and few even that are prominently striped with color—because the factor concerned changes to a factor for self color comparatively rarely." The medium variegated type has more self-colored seeds because the factor for medium variegation, V_mV_m, more frequently changes to the self color condition.

EMERSON concludes that there is a series of nine or ten multiple allelomorphs to which variegation belongs and that these various factors are a result of several mutations from an original factor. Some of these factors mutate frequently, others rarely and still others have never been observed to mutate. The more distinct types of variegation are inherited in a simple Mendelian way, without apparently any evidence of contamination.

EMERSON has used the term sporophytic variation in the place of somatic variation for that class of changes which occur in meristematic cells from which later arise the germ cells as well as the somatic tissues in which the variation is exhibited.

THE MATERIAL USED AND METHOD OF ATTACK

The material used for the present study belongs to the subspecies *Zea mays indurata*. It was known as "Brindle flint" and did not prove to be homozygous for the character from which it takes its name. The mosaic pericarp is formed by either narrow or broad red stripes extending irregularly from the point of attachment of the silk. The ear appears as dark, medium, or light, mosaic, with the variation in number and width of these red slashes.

As the material did not breed true for the character to be studied (1909-'10) it was decided to attempt the production of homozygous races by self-fertilization.

The field technique has been described in a previous publication (EAST and HAYES 1911). At this time a determination was made of the degree of experimental error during pollination. Twenty-five ears were handled in the same way as if pollination was to be made, with the exception that no pollen was applied. Of these twenty-five ears 16 produced no seeds; three ears produced one seed each; four ears produced two seeds each; while one ear produced five seeds. Thus the experimental error is probably less than one seed per ear with a maximum error of five to six seeds per ear.

For the first six years (1909-1914) the work was carried on at the CONNECTICUT EXPERIMENT STATION. Since 1915 it has been conducted at the MINNESOTA EXPERIMENT STATION.

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CONTINUOUS SELECTION FOR TYPE

The first two years of the experiment (1909-10) showed that all ranges of variation from dark, heavily striped ears to colorless-pericarp ears could be obtained. It is worthy of note that no self red ears appeared in either year in a total progeny of 188 ears.

From 1911 to 1916 selection experiments were carried on for the purpose of isolating pure types. The parental ears used were self-pollinated in all cases. Eight classes were used for the description of the progeny according to the amount of variegation of the ears obtained. These classes for pericarp color were: Self red, deep mosaic some seeds self, deep mosaic, medium mosaic, light mosaic, few seeds striped, very slight pattern, and colorless. In addition a record of bud sports was kept showing the somatic variation involved. The self red class consisted of ears in which all seeds were uniformly covered with a red pericarp. In the deep mosaic some seeds self class were placed all ears in which a portion of the seeds were very heavily striped, the remaining seeds having a self red pericarp. The classes, deep mosaic, medium mosaic and light mosaic were used for those ears in which a considerable portion of the seeds were striped with deep red. The number and width of these stripes determined the class in which ears were placed. The class, few seeds striped, consisted of ears in which from 1 to 50 seeds had a few stripes of deep red on the pericarp. The class, very slight pattern, consisted of ears which showed no deep red stripes on the pericarp, but which nevertheless seemed to have a slight color in the pericarp. Microscopical examination showed some reddish coloration in a portion of the cells while other pericarp cells appeared to have no coloring matter. The colorless class consisted of ears in which there appeared to be no color in the pericarp.

It is realized that in a number of these classes no sharp distinction exists. For example the classes deep mosaic, medium mosaic and light mosaic grade into each other. There is also some difficulty in separating the classes, very slight pattern, and colorless. Those ears in which this

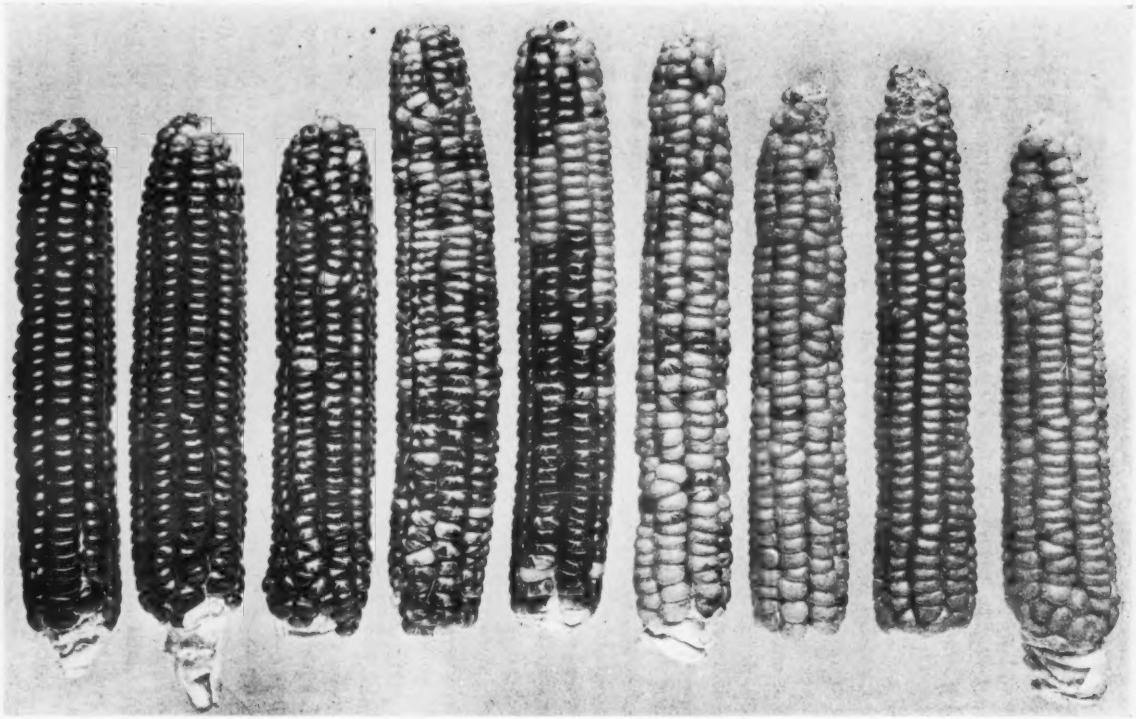

FIGURE 1.—The various types of pericarp color dealt with in this paper. From left to right they represent, respectively, self red, deep mosaic some seeds self, deep mosaic, medium to light mosaic, bud sport, very light mosaic, few deep stripes, pattern color and colorless. (Photograph by HORTON.)

TABLE 1. *Results obtained for pericarp color from self-fertilized ears of Brindle Flint maize*

Ear No.	No. gen. selfed	Progeny classes for color of pericarp									Bud sport	
		Type of parent ear	Self red	Deep mosaic some seeds self	Deep mosaic	Medium mosaic	Light mosaic	Few seeds striped	Very slight pattern	Colorless	Medium—light	Medium—few stripes
(69												
(69-6)	1	Deep mosaic		20 dark and light mosaic	38 mosaic		20 non-mosaic (pericarp pattern and colorless)					
							13 non-mosaic (pericarp pattern and colorless)					
(69-5)	1	Medium mosaic		74 dark mosaic			23 non-mosaic (pericarp pattern and colorless)					
(69-6)-4	2	Deep mosaic			11	24		4	23			
(69-6)-4-2	3	Deep mosaic		11	6	25	6		16			
(69-6)-4-2-6	4	Medium mosaic		4	6	32	10		14		2	
(69-6)-4-2-6-8	5	Medium mosaic	2	8	4	18	1		13		1	
(69-6)-4-2-6-8-5	6	Medium mosaic				17	4	2	4			
(69-6)-4-2-6-8-2	6	Pattern							20			
(69-6)-4-2-6-8-2-7	7	Pattern			5	5	1		23			
(69-6)-4-1	3	Pattern							72			
(69-6)-4-1-6	4	Pattern							67			
(69-6)-4-1-6-2	5	Pattern						1	35			
(96-6)-4-1-6-8	5	Pattern							45			
(69-6)-5	2	Medium mosaic	9		19			10				
(69-6)-5-7	3	Deep mosaic	13	1	11	28	4	2				
(69-6)-5-7-5	4	Medium mosaic	17		5	19	7	13				
(69-6)-5-7-5-6	5	Medium mosaic	7		6	11	4	1				
(69-6)-5-7-5-6-4	6	Medium mosaic				8	1					
(69-6)-5-6	3	Few stripes				1	24	34				
(69-6)-5-6-7	4	Few stripes				6	16	19				
(69-6)-5-6-7-2	5	Light mosaic			2	3	24					
(69-6)-8	2	Medium mosaic				20	1	1				
(69-6)-9	2	Deep mosaic				51		7	13			
(69-6)-10	2	Light mosaic		19	1	34		1				
(69-6)-10-1	3	Deep mosaic some seeds self	7	25		8						
(69-6)-10-1-5	4	Self red	36	4								
(69-6)-10-1-5-1	5	Self red	47									
(69-6)-10-1-5-1-13	6	Self red	63									
(69-6)-10-1-5-1-2	6	Self red	13									
(69-6)-10-6	3	Deep mosaic	7	25		8						
(69-6)-10-6-4	4	Self red	35									
(69-6)-10-6-4-1	5	Self red	27									
(69-6)-10-6-4-1-11	6	Self red	48									
(69-6)-10-6-4-5	5	Self red	25									
(69-6)-10-6-4-5-7	6	Self red	14									
(69-6)-12	2	Medium mosaic			30				3	14		
(69-6)-13	2	Medium mosaic				18	18	8	2			
(69-6)-16	2	Medium mosaic				12		2	3			
(69-6)-14-3	3	Self red	52	6	3							
(69-6)-14-3-1	4	Self red	36	5	3							
(69-6)-14-3-2	4	Self red	55	4								
(69-6)-14-3-3	4	Self red	62	11	1							
(69-6)-14-3-5	4	Self red	54									
(69-6)-14-4	3	Medium mosaic	1	7	5	11	8					
(69-6)-14-4-6	4	Medium light mosaic				5	9	22	2			
(69-6)-14-4-6-1	5	Few stripes					3	27				
(69-6)-14-5	3	Medium mosaic				32			6			
(69-6)-14-5-6	4	Medium mosaic	20	5	11	31	12	2				
(69-6)-14-5-6-8	5	Deep mosaic some seeds self	22	20	6	7	1					
(69-6)-14-5-6-8-6	6	Self red	73	1								
(69-6)-14-5-6-8-6-1	7	Self red	73									

(69-6)-17	2	Medium mosaic	1	7		12	7	13					
(69-6)-17-3	3	Deep mosaic	8	4		4							
(69-6)-17-8	3	Medium and deep mosaic	2		10	23	12	29				6	2
(69-6)-17-8-3	4	Deep mosaic			17	22		4					
(69-6)-17-8-3-4	5	Medium and deep mosaic			11	33	1	5				2	
(69-6)-17-8-3-4-8	6	Medium mosaic			6	20	6	4					
(69-6)-17-8-3-4-8-7	7	Medium mosaic			5	4		1					
(69-6)-17-8-3-4-7	6	Medium mosaic				23	5	3					
(69-6)-17-8-3-4-7-5	7	Medium mosaic			9	6	3	3					
(69-6)-17-8-4	4	Few stripes				4	20	37					2
(69-6)-17-8-4-7	5	Few stripes						20					1
(69-6)-17-8-3-4-2	6	Medium mosaic				35		8	12				
(69-6)-17-8-3-4-2-4	7	Medium mosaic			6	3	7	7	7				
(69-6)-17-8-3-4-2-5	7	Few stripes			1	1	1	1	1				
(69-6)-18-8	3	Medium mosaic				22		5	3				
(69-6)-18-8-3	4	Medium mosaic			3	22	2	6	7				2
(69-6)-18-8-3-2	5	Medium mosaic				18	30	3					
(69-6)-18-8-3-2-10	6	Light mosaic				26	3	3	6				
(69-6)-18-8-3-2-2	6	Light mosaic				10	20	5					
(69-6)-18-8-3-2-10-1	7	Few stripes					1	1	2				
(69-6)-18-8-3-2-10-2	7	Light mosaic				2	17	5					
(69-5)-1	2	Medium mosaic				18	3			3			
(69-5)-1-2	3	Medium mosaic				75		21					
(69-5)-1-2-2	4	Medium mosaic			11	30	2	11					
(69-5)-1-2-2-8	5	Medium mosaic			5	18		1					
(69-5)-1-2-2-86	6	Medium mosaic	1			6	12	2					
(69-5)-1-2-2-86-5	7	Medium mosaic		1	3	3	5	1	1				
(69-5)-2	2	Medium mosaic				40	5			2			
(69-5)-3	2	Medium mosaic			41		3	3		1			
(69-5)-8	2	Light mosaic				11	12	4		5	1		
(69-5)-8-3	3	Colorless							2	1	51		
(69-5)-8-3-5	4	Colorless					3	4		9	20		
(69-5)-8-3-5-1	5	Colorless							2		33		
(69-5)-8-3-5-2	5	Colorless									30		
(69-5)-8-3-5-2-8	5	Colorless							2		29		
(69-5)-8-3-5-2-7	6	Colorless									45		
(69-5)-8-3-5-2-8	6	Possibly pattern									25		
(69-5)-9	2	Light mosaic					36	7					
(69-5)-99	3	Light mosaic					50	30					
(69-5)-99-5	4	Light mosaic				12	51	6					
(69-5)-99-6	4	Light mosaic				4	34	3					
(69-5)-99-2	4	Light mosaic					44	11					
(69-5)-99-2-2	5	Few stripes				6	8	28					
(69-5)-99-2-5	5	Medium to light				36	5	13					
(69-5)-99-2-2-11	6	Few stripes				1	25	7					
(69-5)-99-2-5-4	6	Light mosaic					46	6					
(69-5)-99-2-5-4-1	7	Medium mosaic				1	5	2					
(69-5)-99-2-5-10	6	Medium mosaic				2	46	3					
(69-5)-99-2-5-10-1	7	Medium mosaic				2	20	2					
(69-5)-99-2-5-14	6	Light mosaic				4	32						
(69-5)-99-2-5-14-3	7	Medium mosaic				2	22	12					
(69-5)-99-2-5-14-8	7	Medium mosaic				3	12	2					
(69-5)-99-1	4	Few stripes				1	35	15					
(69-5)-99-1-5	5	Medium mosaic				8	36						
(69-5)-99-1-7	5	Few stripes				14	7	31					
(69-5)-99-1-5-5	6	Medium mosaic				16	17	3					

seemed impossible are placed half way between the two class headings in this table.

While it is possible that some variation may occur, due to a changing ideal as to the value of a particular class, the classification given serves its purpose as it differentiates between heavily striped ears and ears in which the seeds are less heavily splashed with red striations.

The classes self red, deep mosaic some seeds self, and few seeds striped, are of a more distinct type and present little difficulty as regards uniform classification.

Table 1 gives the results obtained from the self-fertilized ears, the progeny of each ear being given separately. Column 1 under Ear No. gives the pedigree of the ears grown, column 2 gives the number of generations that the particular line has been self-fertilized, column 3 gives the type of pericarp of the parental ear while the remaining columns show the range of variation and classification of the progeny of any particular ear.

In a consideration of the results obtained, each pedigree line will be separately discussed.

The progeny for the first two years were not very carefully classified. Beginning with the second generation there is, however, a uniform classification.

The results obtained show a general degree of uniformity for the various types of self-fertilized ears grown. We shall first discuss the families grown from self-fertilized self red pericarp ears.

Family (69-6)-10-6-4 gave a progeny of 35 red ears. Two selections of later generations showed a total progeny of 114 ears all of which had a self red pericarp. The fourth generation selection of family (69-6)-10-1-5 was grown from a self-fertilized self red ear and gave 36 self red ears and 4 in the deep mosaic some seeds self class. As none of the four variegated ears were self-fertilized it was impossible to determine whether they were somatic or germinal variations from the self red type.

One fifth generation and two sixth generation selections gave a total of 123 self red pericarp ears. One third generation family (69-6)-14-3 and three fourth generation lines grown from self-fertilized self red pericarp ears gave a total progeny of 205 self red ears, 26 deep mosaic some seeds self and 7 deep mosaic. One fifth generation family gave a progeny of 54 self red ears.

The sixth and seventh generations of family (69-6)-14-5-6-8-6 gave a total of 146 self red ears and 1 deep mosaic some seeds self ear. In

no case has it been possible to test by breeding experiments the nature of the few deep mosaic ears obtained from self red parentage.

The results given show that the self red ears obtained from variegated parentage tend to give self red progeny. In two families, (69-6)-10-6-4 and (69-6)-10-1-5-1, a total progeny of 233 self red pericarp ears were obtained with no ears in the variegated class.

Two self-fertilized ears of the deep mosaic some seeds self class, (69-6)14-5-6-8 and (69-6)-10-1, behaved as if hybrids between homozygous variegated and pure self red parents, giving a total of 29 self red ears, 45 deep mosaic some seeds self, 6 deep mosaic, 15 medium mosaic, 1 light mosaic, or a total of 67 variegated to 29 self red ears.

This is a ratio per 4 of 2.792 : 1.208. The probable error for this ratio as computed by EAST and HAYES (1911) is ± 0.143. This is, therefore, a fairly close approximation to a 3 : 1 ratio.

The progeny of self-fertilized deep and medium mosaic ears can be placed in four groups: *Group* 1, in which the progeny ranges from self red ears to ears with a few seeds striped, the proportion of self red ears being about one-third of the total progeny; *Group* 2, in which the progeny show only a few isolated cases of the production of self red ears, the remainder being variegated ears; *Group* 3, in which the range of variation is from self red ears to ears with a very slight pattern; *Group* 4, which gives ears ranging from medium mosaic to the few seeds striped class.

Group 1 is represented by the progeny of (69-6)-5, 4 other selections of later generations of this line, (69-6)-10-6 and (69-6)-14-5-6. The total progeny of these self-fertilized parental ears is as follows: 73 self red ears, 31 deep mosaic some seeds self, 52 deep mosaic, 105 medium mosaic, 28 light mosaic and 38 few seeds striped. This makes a total of 254 variegated to 73 self red ears or a ratio per 4 of 3.107 : 0.893. The deviation from a 3 : 1 ratio is 0.107 and the computed probable error ± 0.065.

Of the variegated ears 13 percent were placed in the deep mosaic some seeds self class and 20 percent in the deep mosaic class. The variegated ears, obtained from self-fertilized deep mosaic some seeds self parental ears previously mentioned, gave 67 percent of the variegated ears in the deep mosaic some seeds self class and 9 percent in the deep mosaic class. These results show that self-fertilized ears of the deep mosaic some seeds self type give a larger percentage of deep mosaic some seeds self ears than is obtained from self-fertilized deep or medium mosaic ears.

Group 2 consists of family (69-5)-1 and five selections of later gener-

ations. The progeny consisted of the following ears:—1 self red, 1 deep mosaic some seeds self, 19 deep mosaic, 150 medium mosaic, 22 light mosaic, 36 few seeds striped and 1 very slight pattern and 3 either colorless or very slight pattern.

Disregarding the very slight pattern ears, the proportion of self red ears to variegated is in the ratio of 1 to 77.3. It is possible that ear (69-6)-18-8-3 also belongs to this group, although 7 ears were classified as very slight pattern.

Group 3 may be represented by family (69-6)-4 and four selections of later generations. The progeny of these self-fertilized deep and medium mosaic ears consisted of ears as follows:—2 self red, 23 deep mosaic some seeds self, 27 deep mosaic, 116 medium mosaic, 21 light mosaic, 6 few seeds striped, 47 very slight pattern and 23 which were classed as either very slight pattern or colorless.

Considering the doubtful ears as belonging to the very slight pattern class there is a ratio per 4 of very slight pattern to variegated and self red pericarp ears of 1.057:2.943. The deviation from a 1:3 ratio is 0.057 and the probable error $\pm$ 0.072.

Group 4 may be represented by some generations in family (69-5)-9 in which the range of variation of the progeny consists of the three classes medium mosaic, light mosaic and few seeds striped.

Family (69-5)-9 and later generations consist of a progeny of 181 few seeds striped ears, 531 light mosaic ears and 112 medium mosaic ears. As no ears of a higher grade than medium mosaic or a lower grade than few seeds striped were obtained it will be noted that this family is homozygous for variegation.

The question at once suggests itself: Do self-fertilized ears of the few seeds striped class give a larger proportion of progeny of this grade than self-fertilized medium mosaic ears? As a means of answering this question table 2 has been prepared from the data given in table 1. The percentage of ears of the different grades, medium mosaic, light mosaic and few seeds striped, is given in the table. In discussing these results it should be stated that there is no sharp border line between these different classes. The class few seeds striped is, however, of a more definite type than the other two classes.

A careful study of table 2 shows that self-fertilized medium or light mosaic ears give a smaller percentage of few seeds striped progeny than is obtained from self-fertilized few seeds striped ears. As neither grade, medium mosaic nor few seeds striped, breeds true, and as no definite

TABLE 2

Selection experiments within family (69-5)-9 which bred true for a range of variation from medium mosaic ears to ears with a few seeds striped.

Parentage	Generation	Type of parent ear	Progeny		
			Percent of medium mosaic ears	Percent of light mosaic ears	Percent of few seeds striped ears
69-5-9-9-5	4	Light mosaic	21	71	8
69-5-9-9-5		Light mosaic	10	83	7
69-5-9-9-2		Light mosaic	0	80	20
69-5-9-9-1		Few seeds striped	2	69	29
69-5-9-9-2-5	5	Medium to light	66	9	25
69-5-9-9-2-2		Few seeds striped	19	25	56
69-5-9-9-1-5		Medium mosaic	18	82	—
69-5-9-9-1-7		Few stripes	27	13	60
69-5-9-9-1-5-5	6	Medium mosaic	44	48	8
69-5-9-9-2-5-10		Medium mosaic	4	90	6
69-5-9-9-2-5-14		Light mosaic	11	89	0
69-5-9-9-2-5-4		Light mosaic	—	88	12
69-5-9-9-2-2-11		Few stripes	—	79	21
69-5-9-9-2-5-10-1	7	Medium mosaic	8	84	8
69-5-9-9-2-5-14-3		Medium mosaic	6	61	33

ratios are obtained, these results do not appear to be of the usual Mendelian type of segregation.

Self-fertilized ears of the very slight pattern type are represented by ear No. (69-6)-4-2-6-8-2, one selection of a later generation, ear No. (69-6)-4-1 and three selections of later generations. In one case ear No. (69-6)-4-2-6-8-2-7 a considerable percentage of variegated ears were obtained. These may possibly be due to accidental causes. The other self-fertilized ears gave a total progeny of 240 ears of which 239 were of the very slight pattern type, while 1 showed a single deep red stripe on one seed.

It seems reasonable to conclude, therefore, that ears can be isolated which are homozygous for slight pattern. There is, however, the possibility of a gradual cumulative effect and thus the production of an occasional ear of a higher grade of variegation.

Family (69-5)-8-3 and six selections of later generations consisted of self-fertilized colorless pericarp ears. Four ears of the very slight pattern type, 7 of the light mosaic and few seeds striped class, and 263

colorless pericarp ears were obtained. As none of the variegated ears were selfed it is impossible to say how they would breed.

RESULTS OF SELECTION EXPERIMENTS

1. Selection experiments with a mosaic pericarp pattern color of corn have isolated the following types which breed comparatively true:

(a) A self red pericarp;

(b) Pure for variegation but giving a range of variability from ears with only a few seeds with deep red stripes to ears in which nearly all seeds are quite heavily covered with red striations;

(c) A type with a very slight pattern color which under the microscope appears to be due to the presence of a faint color in some of the pericarp cells;

(d) An uncolored pericarp race.

2. Selection within type (b) which breeds true for variegation has not succeeded in isolating strains which breed true for amount of variegation. Extreme minus types within this strain tend to give a progeny containing more ears of the minus type than are obtained from extreme plus types.

3. Heavily striated self-fertilized ears have proven to be heterozygous, giving a progeny which exhibits segregation for one factor difference.

4. The very deeply variegated heterozygous self-fertilized ears give a progeny in which a greater proportion of the variegated segregates are deeply variegated than is obtained in the progeny of less deeply variegated self-fertilized heterozygous ears.

CROSSES BETWEEN SELECTED TYPES

After isolating several comparatively pure types by selection it was decided to determine their mode of inheritance and relationship to each other by crosses between these various types. For convenience the various crosses will be considered as families and discussed separately.

Family 1. Reciprocal crosses between the self red pericarp type and the homozygous variegated type which exhibited a range of variation from medium mosaic ears to few seeds striped ears

The results from this cross are presented in table 3. Three F_1 crosses are given in the table, reciprocal crosses giving like results. A total of 15 deep mosaic and 84 medium mosaic ears were obtained in the F_1 generation. Five F_1 self-fertilized ears gave the same sort of segregation in F_2. A total progeny was obtained of 98 self red ears, 89 deep

TABLE 3

First and second generation of cross between self red selection (69-6)-10-6-4 *and* (69-5)-9-9, *a selection which breeds true for a range of variation between medium mosaic ears and ears with a few seeds with deep red stripes. Back-crosses of* F_1 *with the parental lines.*

Cross	Generation	Progeny classes				
		Self red	Deep mosaic	Medium mosaic	Light mosaic	Few seeds striped
(69-6)-10-6-4-1-10 × (69-5)-9-9-2-5-4 = 1D	F_1		2	55		
(69-6)-10-6-4-5-3 × (69-5)-9-9-1-5-2 = 3D	F_1		12	13		
(69-5)-9-9-2-2-6 × (69-6)-10-6-4-5-7 = 2D	F_1		1	16		
1 D – 2	F_2	24	26	23	19	2
1 D – 5	F_2	27	13	25		1
2 D – 6	F_2	11	19	21	18	6
2 D – 5	F_2	17	16	34	11	5
3 D – 6	F_2	19	15	48	21	7
2 D – 1 × (69-5)-9-9-2-5-14-1	F_1×variegated parent		17	[a]42[1]	33	9
2 D – 1 × (69-6)-10-6-4-5-7	F_1×self red parent	42	18	27		1

[1] a = ear bud sport one-half medium mosaic one-half few stripes.

mosaic ears, 151 medium mosaic ears, 69 light mosaic ears and 21 few seeds striped ears. This is a ratio per 4 for variegated to self red of 3.084 : 0.916. The probable error in this case is ± 0.056.

One F_1 generation ear was pollinated by the variegated parent and gave a progeny of 17 deep mosaic, 41 medium mosaic, 33 light mosaic, 9 few seeds striped, and 1 bud sport, a part of the ear being medium mosaic, the other part belonging to the few seeds striped type.

The back-cross of the F_1 with the self red parent gave 42 self red ears, 18 deep mosaic ears and 27 medium mosaic ears.

The results obtained from the F_2 generation and the crosses of F_1 with the parental types, respectively, show that one main factor difference is involved. If we consider these factors as *M* and *S* respectively, we may conclude that *M* and *S* are allelomorphs or according to MORGAN's chromosome hypothesis, located in corresponding loci of homologous chromosomes.

Family 2. First and second generation crosses of homozygous self red pericarp and pattern selections

The same self red races were used as for the cross between self red and homozygous variegated described in the previous family. The F_1 generation cross of the self red with the pattern selection consisted of self red ears and in F_2 109 self red ears, 39 pattern ears and 1 ear with one deep red stripe on one seed was obtained. This is a clear indication of a 3 : 1 ratio.

Comparing these results with family 1 shows a complete dominance of the self red pericarp in one cross and an intermediate condition in the other cross. There is a greater difference in character between the self red and pattern types than for the self red and variegated selections. Complete dominance was obtained in the cross in which the parental varieties differed most widely.

TABLE 4

First and second generation of cross between selection (69-6)-4-1-6-2-7 and (69-6)-4-1-6-8-3, which breed true for pattern color, and (69-10)-1-5-1-2 and (69-10)-6-4-5-1, selections which breed true for self red pericarp.

Cross	Generation	Progeny classes	
		Self red	Pattern
(69-6)-4-1-6-2-7 × (69-10)-1-5-1-2 = 1 B	F_1	58	
(69-6)-4-1-6-8-3 × (69-10)-6-4-5-1 = 2 B	F_1	All self	
1 B – 8	F_2	53	[a]21[2]
2 B – 1	F_2	56	19

[2] a = Deep red stripe on one ear.

Family 3. First and second generations of the cross between the pattern selection and the variegated type

The parental types are the recessive selections of the crosses given in families 1 and 2. *MM* represents the selection which proved to be homozygous for the variegated character. Table 1 shows a total progeny of 324 ears obtained in family (69-5)-9 all of which were of the variegated type. *PP* represents the pattern type, (69-6)-4-1-6, which bred true to the pattern condition. These two selections when crossed with the self red pericarp type showed the ordinary Mendelian expectation in F_2 for one factor difference.

The results obtained for the cross between variegated and pattern selections are presented in table 5.

The F_1 generation consisted of 143 variegated ears and 1 ear of the pattern type. Of the variegated ears 5 were classed as deep mosaic which is a higher grade than was obtained in the homozygous variegated parent and 4 were classed as bud sports. As no bud sports appear in either of the homozygous parental varieties, it would seem as if crossing has in some way produced a condition of instability. This instability is also shown by the increased variability obtained in F_1 from crossing apparently homozygous types.

Nine self-fertilized F_1 ears were grown in F_2. Three of these ears were of the bud sport type, while of the other six 5 were classed as light mosaic and one as medium mosaic. The three ears classed as bud sports gave a total progeny of 188 ears, 10 of these being bud sports. The "non-sport" ears gave a total progeny of 445 ears, 11 of which were bud sports. The ratio of bud sport ears from self-fertilized bud sport parentage is 1 bud sport to 18.8 normal. When normal ears were planted 1 of the bud sport type was obtained to 40.4 ears of the normal type.

The F_2 generation exhibits a greater variability than the F_1. Nine F_1 self-fertilized ears gave a total progeny in F_2 of 12 self red ears, 420 variegated ears ranging from deep mosaic some seeds self to ears with only a few seeds striped with deep red, 21 which exhibited sharp segregation of characters on the ear, a part of the ear being of one type, the remainder being of another type and 201 ears of the pattern type.

This is a total of 201 pattern ears to 453 of the variegated and self red classes or a ratio per 4 of pattern ears to other sorts of 1.229:2.771.

TABLE 5

First and second generation of cross between selection (69-6)-4-1-6 which breeds true for the pattern pericarp, with selection (69-5)-9-9-2 which breeds true for a range of variation from medium mosaic ears to ears with a few seeds striped.

Cross	Generation	Type of parent ear	Progeny classes							Bud sports					
			Self red	Deep mosaic few seeds self	Deep-mosaic	Medium mosaic	Light mosaic	Few seeds striped	Pattern	Medium—light	Medium—few seeds striped	Deep—light	Light—few seeds striped	Medium—pattern	Light—pattern
(69-6)-4-1-6-2-12 × (69-5)-9-9-2-5-6 = 4 A	F_1				5	21	3	1				1			
(69-6)-4-1-6-8-1 × (69-5)-9-9-2-2-4 = 3 A						10	20	2	1			1			
(69-6)-4-1-6-2-11 × (69-5)-9-9-2-2-10 = 2 A						14	23	10		1					
(69-6)-4-1-6-8-2 × (69-5)-9-9-2-2-1 = 1 A						10	15	5		1					
Total	F_1				5	55	61	18	1	2		2			
1 A — 1	F_2	Bud sport medium —few stripes			3	7	12	4	16		1				
1 A — 5		Bud sport	1			4	14	8	8		3		2		
1 A — 2		Light mosaic			3	13	20	12	17				2		2
1 A — 3		Light mosaic			3	8	24	14	22		4				
2 A — 5		Light mosaic	4	1	5	17	20	10	28		1			1	
3 A — 3		Light mosaic	7	3	5	18	20	9	24		1				
3 A — 6		Light mosaic			4	14	25	14	33						
4 A — 2		Bud sport				13	28	23	37		1			1	2
4 A — 3		Medium mosaic			3	8	27	4	16						
Total	F_2		12	4	26	102	190	98	201		11		4	2	4

Family 4. First and second generation of cross between the homozygous variegated and colorless selections

The results of this cross are presented in table 6. The F_1 generation consisted of 41 variegated ears. In F_2 103 variegated, 17 pattern, and 28 colorless pericarp ears were obtained. One of the variegated ears was of a higher grade than the F_1 or variegated pattern type. The nature of these 17 pattern ears could only be determined by breeding test, which was impossible, as none of these ears happened to be selfed.

As only a single cross between variegated and colorless has been studied, it does not seem wise to make an extended discussion of these results. The deviations from simple Mendelian expectations might be explained by supposing the variegated factor *M* to change to a factor for self color *S* or to the pattern factor *P*. It is equally possible that these results might be explained by accidental chance pollination.

RESULTS OF CROSSING HOMOZYGOUS TYPES

1. The cross between the self red selection *SS* and the homozygous variegated type *MM* gave an intermediate F_1 which consisted of ears which were more deeply striated than the homozygous variegated race. The F_2 generation grown from self-fertilized F_1 ears showed a segregation of self red, F_1, and homozygous types, as expected for one unit-factor difference. Back-crosses of the F_1 with the parental strains gave parental and F_1 types in a 1 : 1 ratio.

2. The cross between the self red selection *SS* and the pattern selection *PP* showed a dominance of the self red type in F_1 and in F_2 a segregation of self red and pattern types in a 3 : 1 ratio.

3. The cross between the homozygous variegated selection *MM* and the pattern selection *PP* gave an increase of variability in F_1 which was shown by ears of a higher grade for variegation than the parental variegated race and by the production of a considerable proportion of bud sport ears. In F_2 some self red ears were obtained. The proportion of pattern ears to other grades was 1 to 2.3.

4. The cross between the homozygous variegated race, *MM*, and the colorless race, *CC*, gave F_1 ears of the variegated type and a segregation in F_2. One ear of a higher grade than the F_1 and a number of ears of the pattern type were obtained as well as a considerable number of ears of the two parental types.

TABLE 6

First and second generation of cross between colorless pericarp selection (69-5)-8-3-5-2-3 and light mosaic selection (69-5)-9-9-2-5-5.

Cross	Gen.	Progeny classes						
		Deep mosaic few seeds self	Deep mosaic	Medium mosaic	Light mosaic	Few stripes	Pattern	Colorless
(69-5)-8-3-5-2-3 × (69-5)-8-8-2-5-5 = C	F_1			13	25	3		
C — 6	F_2	1		13	35	7	11	14
C — 7	F_2			6	35	6	6	14

DISCUSSION AND INTERPRETATION OF RESULTS

The results presented in the experiments are of two sorts:

1. Those which show the usual type of Mendelian inheritance, i.e., dominance, recessiveness, and segregation with definite ratios.

2. Results which are not easily explained by the hypothesis of absolute purity of fundamental factors of inheritance.

The use of several main factors is helpful in an explanation of the Mendelian results obtained. The letters *S* and *M* respectively denote factors for self color and variegation. The letter *P* may be used to denote the very slight pericarp pattern factor which in the absence of *M* or *S* produces a slight pattern color. This appears to be a true pattern factor as a portion of the cells of the pericarp of a homozygous very slight pattern race show a slight color while other cells appear to contain no coloring matter.

Selection experiments served to isolate races which bred comparatively true for the following pericarp characters: Self red, *SS*, homozygous variegated, *MM*, very slight pattern, *PP*, and colorless, *CC*. The crosses between self red, *SS*, very slight pattern, *PP*, and self red with homozygous variegated, *MM*, showed that these factors are distinct in inheritance. The ratio obtained for the F_2 of the self red—pattern cross was 3 : 1 and for the self red—variegated cross was 1 : 2 : 1. The fact that no new types were produced by these crosses would indicate that *P*, *M* and *S* were multiple allelomorphs. It is impossible to say which is the normal condition from which the other types were produced.

The cross between *MM* and *PP* gave results of a different nature. Before discussing these results it may be well to discuss the evidence for purity of the parental types used. Before making the cross the parental varieties were self-pollinated for several generations. The progeny of the self-fertilized ears of the slight pattern type, *PP*, consisted of 219 ears of the pattern type and 1 ear with a single deep red stripe on one seed. As this ear was open-pollinated it was impossible to determine whether or not this was a germinal variation. The variegated family (69-5)-9 and later self-fertilized generations showed a total of 824 ears all of which were of the variegated type. No ears were produced which did not have a deep red stripe on at least one seed and no ears which were of a higher grade than the medium mosaic class. Within this family self-fertilized medium and light mosaic ears tended, however, to give a larger proportion of ears in the medium and light mosaic class than self-fertilized few stripe ears. Seeds of 6 self-fertilized medium

mosaic ears which were grown in four successive generations did not materially decrease the range of variegation. Somewhat similar results were obtained in the progeny of 5 self-fertilized light mosaic ears and in the progeny of 3 self-fertilized few stripe ears. There is also no marked uniformity of results for the different types of self-fertilized ears and no indication of definite segregation. These results could be brought into line with EMERSON'S by supposing a separate factor for medium variegation M_m which is allelomorphic to a factor for light variegation M_l and by further supposition of frequent germinal variations of M_l to M_m and *vice versa*.

As this family breeds true for variegation, we may conclude that it is homozygous for a factor for variegation, or MM (= "mosaic"). The hypothesis of slight germinal variations for the variegated factor seems to be a simpler explanation of the results obtained than the supposition of a definite change from M_l to M_m.

The cross between the variegated type and the very slight pattern type showed a dominance in F_1 of the variegated race. There was also an increase in variability in F_1 and ears of a higher grade of variegation were obtained than in the progeny of the homozygous variegated parent. Table 1 shows that no bud sport ears were obtained in the homozygous parental selections. The F_1 generation of the cross, however, showed 4 ears of the bud sport type in a total of 144 ears. This is between 2 and 3 percent.

The F_2 generation of this cross gave a little over 36 percent of the progeny in the pattern class, 58 percent of the variegated type, 2 percent bud sports and 4 percent self red pericarp ears. As four different crosses between the pattern and variegated races were studied and as results were of the same nature for each cross, they seem fairly dependable.

If M and P were not allelomorphs some F_2 combinations would lack both M and P and presumably lack color in the pericarp. As no such ears were obtained and as there is considerable evidence which seems to show that M and P are respectively allelomorphic to the factor for self color, S, there seems to be sufficient reason for concluding that M and P are allelomorphs.

We may then suppose that the union of M and P in F_1 causes some sort of contamination which produces a condition of instability. In some cases the M factor may change to the self red form, S. The instability of this zygotic combination MP is further shown by the pro-

duction of a considerable proportion of bud sport ears. As few sports (none having been observed) are produced in the self-fertilized parental forms, *MM* and *PP*, one might conclude that certain heterozygous combinations produce germinal instability which exhibits itself either as imperfect segregation, gametic contamination or sporophytic variation.

SUMMARY

Variegated or pattern characters have generally been considered to be of unstable nature. Self-fertilization and selection within a red mosaic pericarp pattern color of maize isolated several types which bred relatively true. The types for pericarp color were self red, variegated, pattern and colorless. Evidence is given which shows that the self red, pattern and colorless selections are homozygous for these characters. The variegated selection proved to be homozygous for the mosaic character and gave a range from ears in which nearly all seeds were heavily striated to ears in which only a few seeds showed red stripes. Extreme plus ears tended to produce a progeny with more ears of the plus type than was obtained in the progeny of few stripe ears. The range of variation, however, was not affected by such selection. These results are explained by the hypothesis of slight germinal variations.

The relation of these various pericarp characters was then studied by making crosses between the various homozygous types. The cross between self red and variegated gave an F_1 with a more intense variegation than the variegated parent and a ratio of 1 : 2 : 1 in F_2. The self red—pattern cross gave self red ears in F_1 and a ratio of 3 self red to 1 pattern in F_2. The pattern—variegated cross gave an F_1 with a greater range of variation than either parent. Nearly all ears had a variegated pericarp, several being of a higher degree than the variegated parent. The unstable nature of this cross was further shown by the production of a considerable percentage of bud sport ears. A few self red ears were obtained in F_2, many variegated ears, nearly half as many pattern ears, as well as a number of bud sport ears. The suggestion is made that certain combinations produce germinal instability. The conclusion is then reached that the factors for self red, variegated, pattern and colorless pericarp form a series of multiple allelomorphs.

LITERATURE CITED

CORRENS, C., 1910 Der Übergang aus dem homozygotischen in einen heterozygotischen Zustand im selben Individuum bei buntblättrigen und gestreiftblühenden Mirabilis-Sippen. Ber. d. deutsch. bot. Ges. **28**: 418-434.

DEVRIES, HUGO, 1910 The Mutation Theory. Vol. 2, pp. viii+683. Chicago: The Open Court Pub. Co.

EAST, E. M., AND HAYES, H. K., 1911 Inheritance in maize. Connecticut Exp. Sta. Bull. 167. pp. 3-142.

EMERSON, R. A., 1914 The inheritance of a recurring somatic variation in variegated ears of maize. Nebraska Research Bull. 4. pp. 3-35.

1917 Genetical studies of variegated pericarp in maize. Genetics **2**: 1-35.

JENNINGS, H. S., 1916 Heredity, variation and selection in Difflugia. Genetics **1**: 407-534.

STOUT, A. B., 1915 The establishment of varieties in Coleus by the selection of somatic variations. Carnegie Inst. of Washington Pub. No. 218, pp. 80.

SUPPLEMENTARY DETERMINATIONS OF THE RELATIONSHIP BETWEEN THE NUMBER OF OVULES PER POD AND FERTILITY IN PHASEOLUS[1]

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INTRODUCTION

One of the phases of a study of the physiology of seed production which has been under way for the past ten years has been the investigation of the relationship between the number of ovules laid down per pod and the capacity of the pod for maturing these ovules into seeds.

In adequately large series of observations, the value of r_{os}, the correlation between the number of ovules formed, o, and the number of seeds developing, s, per pod, has always been found to be positive. Furthermore, the relationship in Phaseolus, and in some other legumes which have been thoroughly investigated, may be *fairly* satisfactorily represented by the slope of a straight line. In other words, the mean number of seeds matured per pod increases at practically a uniform rate from the lowest to the highest number of ovules formed.

Such a relationship would be expected if the failure of individual ovules to develop into mature seeds were due to purely random causes. Its existence cannot, however, be taken to indicate that the failure of the ovules to develop into seeds is due solely to such causes. The correlation constant r_{os} is of descriptive value only. It may differ significantly from species to species or from environment to environment. Thus the average of the correlation between number of ovules and number of seeds in Staphylea has been shown (HARRIS 1912) to be .0282 for a lot of 20 shrubs from which collections were made in 1906 and .0658 in a series of 16 determinations from individual shrubs in 1907. For Cercis (HARRIS 1914) the correlations are .648 for a series from Meramec Highlands, Mo., .603 for a series from the vicinity of Lawrence, Kansas, and .455 for materials from the neighborhood of Sharpesburg, Ohio. For Sanguinaria (HARRIS 1910) the values are over .800.

[1] Studies on the correlation between morphological and physiological characters. IV.

Many other constants from published and unpublished data might be given, but since they merely serve to illustrate the variability of the correlation between the actual number of ovules laid down and the actual number of seeds developing, further examples are superfluous.

But what is needed in physiological investigations is a measure of the relationship between the number of ovules per pod and the capacity of the pod for maturing these ovules into seeds. This need was first realized and met in 1909, when it was shown by Professor PEARSON and myself (HARRIS 1909) that the relationship between the number of ovules per pod and its capacity for maturing its ovules into seeds may be expressed in terms of the correlation between the number of ovules and the deviation of the number of seeds matured per pod from the probable value, that is from the number which would be expected if it were determined solely by the relative proportion of the ovules which developed into seeds in the population at large, i. e., by $p = \bar{s}/\bar{o}$, where the bars denote population means, and not at all by other factors associated with number of ovules per pod. Three years ago the results of the analysis of the first extensive series of data, comprising countings of over 160,000 pods belonging to 53 series of experimentally grown plants representing six varieties of garden beans, were discussed (HARRIS 1913). Since that time numerous data for an arborescent legume, *Cercis Canadensis,* have also been treated. In a first paper (HARRIS 1914 a), the findings for large samples of pods collected from many trees were set forth. In a second memoir (HARRIS 1914 b), the same data were treated for individual trees. It seems unnecessary to do more in the way of general discussion of the subject than to refer to these publications.

MATERIAL AND METHODS

The data upon which the present discussion is based are those of a preceding paper (HARRIS 1917). The method of determining correlation between the number of ovules formed and number of seeds developing, is the usual one.

The values of the correlation between the number of ovules per pod and the deviation of the number of seeds per pod from its probable value has been computed from the usual formula

$$r_{oz} = \frac{r_{os} - v_o/v_s}{\sqrt{1 - r_{os}^2 + (r_{os} - v_o/v_s)^2}}$$

where v_o and v_s are the coefficients of variation, 100 $\sigma_o/\bar{o}$, 100 $\sigma_s/\bar{s}$, the

sigmas denoting standard deviations and the bars indicating population means.

PRESENTATION OF DATA

In the accompanying table the key letters for the 16 cultures are followed by the number of pods upon which the determinations are based.

Series	N	r_{os} and Er_{os}	r_{oz} and Er_{oz}	r_{oz}/Er_{oz}
HHT	3722	.418±.009	—.040±.011	3.64
HHHT	7429	.382±.007	—.083±.008	10.38
HDT	1600	.382±.014	—.094±.017	5.53
HDDT	6408	.362±.007	—.096±.008	12.00
DDT	1151	.381±.017	—.055±.020	2.75
DDDT	3501	.368±.010	—.078±.011	7.09
DHT	2516	.331±.012	—.118±.013	9.08
DHHT	3412	.334±.010	—.126±.011	11.45
USHT	3772	.294±.010	—.072±.011	6.55
USHHT	3087	.276±.011	—.087±.012	7.25
USDT	2601	.260±.012	—.112±.013	8.62
USDDT	4355	.282±.009	—.095±.010	9.50
FSHT	3127	.249±.011	—.098±.012	8.17
FSHHT	3700	.227±.011	—.128±.011	11.64
FSDT	2531	.294±.012	—.065±.013	5.00
FSDDT	3786	.274±.010	—.109±.011	9.91

The third column gives the correlation between the actual number of ovules and the actual number of seeds per pod. The fourth column contains the results for the correlation between the number of ovules per pod and the deviation of the number of seeds from their probable value on the assumption of the absence of any relationship between ovule number and capacity for seed production. The ratios of these constants to their probable errors—measures of their statistical trustworthiness—appear in the final column.

The correlation between the number of ovules formed and the number of seeds developing is positive throughout, with an average of .3196 ± .0094 and a standard deviation of .0556 ± .0066 as compared with a mean correlation of .3964 ± .0092 and a variability in correlation of .0998 ± .0065 in the first series. Thus the mean correlation in the first series is .0768 ± .0132 higher than in the second, but it must be noted (*a*) that seven varieties are represented in the first series as compared with four in the second, and (*b*) that the environmental

conditions under which the two lots were grown were very different. The variability in correlation is .0442 ± .0092 higher in the first than in the present series of determinations, but this may also be attributed largely if not entirely to greater heterogeneity in varietal composition and in environmental conditions.

Turn now to the values of r_{oz}, the coefficient measuring the relationship between the number of ovules per pod and the capacity of the pod for maturing its ovules into seeds. The constants appear in the fourth column of the table. A measure of their statistical significance, the ratio of the correlation coefficients to their probable errors, is given in the final column of the table. The sign and the magnitude of the constants is also shown graphically in diagram 1, which contains the first 53 as well as the present series. Here the magnitudes of the coefficients, serially arranged, are shown by the length of the lines extending above

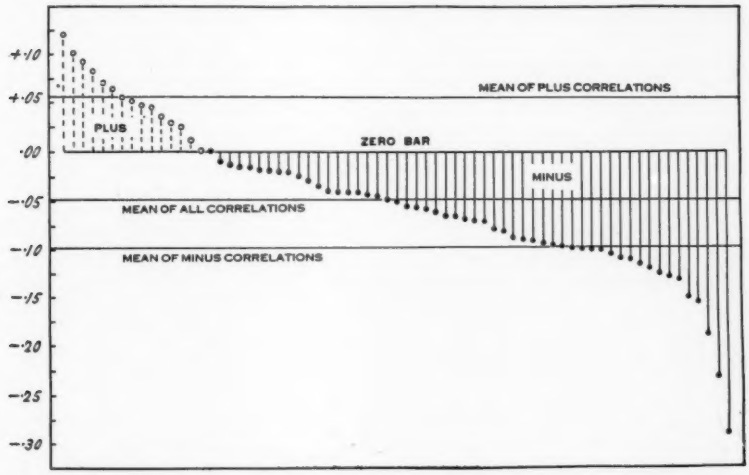

DIAGRAM 1.—Distribution of correlations between number of ovules per pod and the deviation of the numbers of seeds per pod from their probable value.

and below the zero bar for the positive and negative coefficients respectively.

The new series of determinations differs conspicuously from that of the first paper on Phaseolus in that the measurements of the present series are negative throughout. In the first series, 38 were negative and 15 positive in sign.

If the results of the two sets of determinations be combined,[2] it is to be noted that there are 54 negative as compared with 15 positive correlations. This is a deviation from equality (which should be found if there were no biological factors tending to bring about a definite correlation) of

$$(54—34.5) \text{ or } (15—34.5) \pm .67449 \sqrt{69 \times .5 \times .5} = 19.5 \pm 2.80$$

The deviation is over 6.9 times as large as its probable error, and so almost certainly significant.

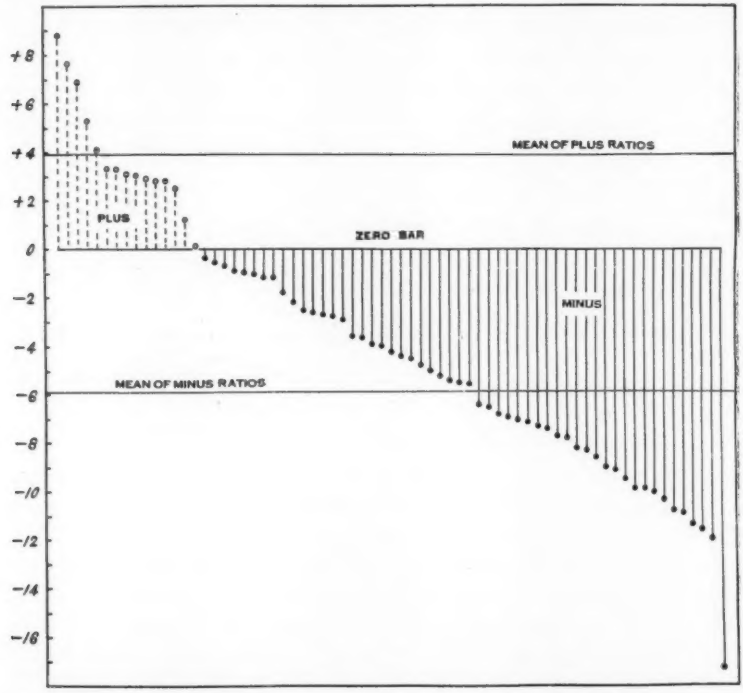

DIAGRAM 2.—Distribution of the ratios of the correlations between the number of ovules per pod and the deviation of the number of seeds per pod from their probable value to the probable errors of these correlations.

[2] While, as emphasized above, the second series of determinations is technically decidedly the better of the two, it does not represent the range of environmental conditions found in the first. That such conditions may influence the relationship here under consideration is perhaps indicated by the differences demonstrated in an earlier paper, for Cercis from Missouri, Ohio and Kansas localities. To avoid all possible criticism as to the selection of data it has seemed wise to consider the two series, both individually and in combination.

Thus if conclusions be based upon the nature of the relationship as indicated by their signs, and without regard to the intensity or statistical trustworthiness of the individual constants, there can be no question concerning the existence of a negative correlation between number of ovules per pod and capacity for seed production.

This conclusion receives substantiation of the most convincing sort from an examination of the relation of the individual constants to their probable errors.

These are shown in the final column of the table of constants and are represented graphically for the 69 determinations available from the first and second series in diagram 2. This is constructed in the same manner as diagram 1, except that the length of the bars indicates the magnitude of the coefficients in relation to their probable errors, i. e., the ratio of the constants to their probable errors.

Of the 69 determinations, 57 are at least 2.5 times as large as their probable errors. Of these, 44 are negative as compared with 13 which are positive in sign. Of the 40 constants which are over 4 times as large as their probable errors, 35 are negative as compared with only 5 which are positive in sign. Finally, there are 24 values which are over 7 times as large as their probable errors. Of these, 22 are negative as compared with 2 which are positive in sign.

Thus, judged by the measures of the statistical significance of the individual constants, there can be no possible question that the negative coefficients are far more trustworthy than are the positive ones. The average ratio of the 54 negative correlations to their probable errors is 5.97 as compared with 3.87 for the positive.

Consider now the actual magnitudes of the correlations.

The constants for correlations (r_{os}) in the two series are:

	Mean	Standard deviation
First series	—.0365±.0075	.0811±.0053
Second series	—.0910±.0040	.0242±.0028
Difference	.0545±.0085	.0569±.0060

Thus the mean value of the correlation is numerically higher and the variability of the correlation significantly less in the second series of determinations. The difference in the means is .0545±.0085, or over 6.4 times as large as its probable error. The standard deviation for the second group of constants is less than a third of that found for the first lot. The actual difference is .0569±.0060, or an amount over 9.4 times as large as its probable error.

This is precisely the result which would be expected if perfection of the experimental and observational conditions resulted in the detection in every instance of a relationship hitherto often obscured by uncontrolled factors. The second series is unquestionably the better of the two. It evidences much more strongly for the existence of a negative relationship between the number of ovules formed and the capacity of the pod for maturing its ovules into seeds.

The constants for the 69 determinations resulting from a combination of the earlier and the present series are:

Mean	$-.0491 \pm .0061$
Standard deviation	$.0786 \pm .0043$

Variety		Number of series	Mean r_{oz}	Mean $r_{oz}/E_{r_{oz}}$
Golden Wax	Plus correlation	—	—	—
" "	Minus correlation	3	−.081	−4.20
" "	All correlation	3	−.081	—
Black Wax	Plus correlation	—	—	—
" "	Minus correlation	2	−.262	−8.49
" "	All correlation	2	−.262	—
Burpees Stringless	Plus correlation	—	—	—
" "	Minus correlation	8	−.055	−5.46
" "	All correlation	8	−.055	—
Navy H	Plus correlation	6	+.074	+5.48
" "	Minus correlation	7	−.061	−6.82
" "	All correlation	13	+.001	—
Navy D	Plus correlation	6	+.050	+3.28
" "	Minus correlation	7	−.070	−5.70
" "	All correlation	13	−.015	—
Ne Plus Ultra	Plus correlation	1	+.071	+2.78
" " "	Minus correlation	14	−.077	−5.56
" " "	All correlation	15	−.067	—
White Flageolet	Plus correlation	2	+.014	+1.35
" "	Minus correlation	13	−.079	−6.41
" "	All correlation	15	−.066	—

The mean value differs from 0 by over 8 times the probable error of the determination. There can, therefore, be no question concerning its significance.

If the determinations be divided into two groups, positive and negative, the averages are:

Positive constants	+.0565
Negative constants	−.0785

The averages for each variety are shown in the accompanying table. Without exception there are more negative than positive correlations in each variety. Without exception the negative correlations show a higher degree of statistical trustworthiness in each variety than do the positive correlations. With the single exception of the Navy H series, in which the mean correlation is positive by an insignificant amount, the mean correlation is negative in sign in each variety.

Thus while the number of determinations for each variety must of necessity be small, the results for the individual strains substantiate in a most striking manner the conclusions drawn from the data as a whole.

DISCUSSION OF RESULTS

The present paper is devoted to the problem of the relationship between the number of ovules formed per pod and the capacity of the pod for maturing these ovules into seeds.

The relationship is measured in terms of the correlation between the number of ovules per pod and the deviation of the number of seeds per pod from the probable number on the assumption that the chances of an individual ovule developing into a seed are quite independent of the number of ovules in the pod in which it is produced. Sixteen new series of data for Phaseolus, comprising countings of number of ovules formed and number of seeds developing per pod in 56698 pods, are presented, and the constants deduced from them compared with those from 53 series comprising 166130 pods published in an earlier paper.

These lead to the conclusion that there is a negative relationship between number of ovules formed per pod and capacity for maturing these ovules into seeds, i. e., that pods with larger numbers of ovules show a relatively lower capacity for maturing their ovules into seeds.

Either of these series taken independently may be considered as establishing the conclusion drawn. The second, however, not merely substantiates the first, but indicates that the law holds even more rigorously than appeared from the first series of data. In the first 53 determinations, only 15 out of 53 constants were exceptions to the rule. In the second series, the results are consistent throughout. In the first series, the mean value of r_{oz}, which should be zero if there were no relationship between number of ovules per pod and capacity for maturing seeds, is negative in sign and about five times as large as its probable error. In the second series, it is negative in sign and over twenty times as large as its probable error. In the first series of determinations, 41 of the 53

constants are at least 2.5 times as large as their probable errors. In the second series each of the 16 constants is at least 2.5 times as large as its probable error, and many are several times as large as their probable errors.

As biological facts, the results presented here seem soundly established, so far as the species in question is concerned, and represent, therefore, one further step in the analysis of the problem of fertility and fecundity in plants. The physiological interpretation of the results is quite another matter. Anyone venturing to suggest explanations must bear in mind that the problem is one involving many factors and surrounded by many difficulties which need not be discussed here. It is reasonable to believe that these difficulties like those which have surrounded the carrying of the investigation up to the present point, will ultimately be overcome by the application of biometric formulae to appropriately collected masses of quantitative data.

LITERATURE CITED

HARRIS, J. ARTHUR, 1909 The correlation between a variable and the deviation of a dependent variable from its probable value. Biometrika **6**: 438-443.

1910 A quantitative study of the fruit of the blood-root, *Sanguinaria Canadensis*. Biometrika **7**: 305-351.

1912 The influence of the seed upon the size of the fruit in Staphylea. Bot. Gaz. **53**: 204-218, 396-414.

1913 On the relationship between the number of ovules formed and the capacity of the ovary for developing its ovules into seeds. Bull. Torr. Bot. Club **40**: 447-455.

1914a On the relationship between the number of ovules formed and the number of seeds developing in Cercis. Bull. Torr. Bot. Club **41**: 243-256.

1914b Further observations on the relationship between the number of ovules formed and the number of seeds developing in Cercis. Bull Torr. Bot. Club **41**: 533-549.

1917 Futher studies on the relationship between bilateral asymmetry and fertility and fecundity in the unilocular fruit. Genetics **2**: 186-204.

SEVERAL COLOR "MUTATIONS" IN MICE OF THE GENUS PEROMYSCUS

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In the course of breeding experiments conducted by the author for more than two years past, certain rather striking "sports" have appeared, which seem to behave as discontinuous hereditary variations. Although sufficient time has not elapsed since their appearance to reveal the exact mode of transmission of these aberrant characters, a brief account of them seems justifiable at present.

PARTIAL ALBINISM

About December 29, 1915, a litter of five young were born, whose parents were brother and sister, both being F_1 hybrids between the subspecies *P. maniculatus sonoriensis* and *P. m. rubidus*. These two subspecies differ conspicuously in color as well as in some other characters, the former race being of a much lighter shade than the latter. Hybrids of the F_1 generation are on the whole intermediate in this respect. Of the five young F_2 mice above referred to, three developed a normal amount of pigment in the skin and eyes, while the other two remained extremely pale. At first glance, this might have been interpreted as a case of simple Mendelian splitting, resulting in the appearance of the grandparental color types. But a close inspection of the pale individuals, as late as the eighth or ninth day after birth, showed that they were nearly or quite pigmentless. Moreover, further breeding of hybrids between these two races has proved that no such simple segregation phenomena occur in the F_2 generation.

Unfortunately, all of the foregoing brood died in very early life, none reaching the age of two weeks. On January 8, 1916, a sister of the above-mentioned mother gave birth to a brood of two, the father being the same as in the preceding case. Both of these F_2 offspring, which are still living, are normally pigmented. But on October 5, 1916, a second litter was born of these same parents. This litter, when first examined, comprized two pale individuals, one of each sex. The skins

of these young mice failed to darken, as happens in normal animals, preceding the outgrowth of the hair, and the pigment of the eyes, which is usually conspicuous at this age, was not in evidence. The hair, at the time of its emergence, appeared nearly white.

Six weeks after birth, these mice, which were still in juvenal pelage, were covered, on the dorsal and lateral surfaces, with hair of a very pale gray shade, very near the "drab gray" of RIDGWAY's *"Color Standards,"* though perhaps a trifle paler. (Two normal F_2 hybrids of the same age varied in shade between RIDGWAY's "neutral gray" and "dark neutral gray," perhaps averaging the "deep neutral gray".) Viewed from a distance, in the subdued light of the murarium, the "albinos" did not differ widely in appearance from ordinary white mice, but the deeper shade was evident when one contrasted the faintly pigmented lateral region of the body with the truly white hair characteristic of the ventral surface of this species. Other peculiarities of these partial albinos are the complete absence of the black dorsal tail-stripe, the nearly white condition of the ears and the reddish color of the eyes. The latter are far from being of the pink hue found in domesticated white mice and rats, but they nevertheless contrast clearly with the jet black eyes of normal Peromyscus. Moreover, they differ notably in size, being smaller, or at least failing to protrude from the head as in the normal animals. Thus the mutation here considered involves several distinct characters, which may, of course, be physiologically related.

At the age of six weeks, a change of pelage was found to be in progress in both of these young mice, though the new hair had not appeared at the surface except in the male. In the latter, the customary replacement of gray by colored hair was evident on the antero-lateral surfaces of the body, but the color in this case was an extremely pale yellow.

Upon the completion of the post-juvenal pelage, some ten weeks after birth, these mice were of a very pale gray shade, suffused with a yellow, which is probably not far from RIDGWAY's "ochraceous buff" or "cinnamon buff." It would be impossible, however, to express their appearance in terms of any homogeneous shade or tint, covering a continuous plane surface. This second pelage is somewhat darker than the first one, as well as of a different color. In these aberrant mice, as in normal ones, the proximal zone of the hair differs in color from the distal, being of a somewhat "sooty" or "slaty" hue, contrasting with the colored tips. This underlying dusky zone is very much paler, however, in these "mutants" than in the more deeply pigmented animals.

CASTLE (1912) has discussed the finding of a "pure white albino" of

Peromyscus leucopus noveboracensis and the subsequent rearing of several specimens in the laboratory. CASTLE's mice evidently differed considerably from my own, which are far from being *pure white*. MORGAN (1911, p. 106) describes some nearly white specimens of *P. leucopus ammodytes*, which appeared among his laboratory stock. These animals were apparently black-eyed, however, and retained part of their dark pelage. MORGAN ascribes these changes to some unknown factor in their unnatural environment, acting during the lifetime of the individuals. Whether or not these "mutants" of mine be regarded as albinos or as "red-eyed yellows" is a matter of slight importance for present purposes. Their peculiarities of color obviously depend upon a loss of most of their normal pigment, and this loss affects all of the colored parts of the body. The condition is one which might reasonably be expected to be hereditary, since it has appeared in only two broods, derived from consanguineous matings, the father being the same in the two cases, and the mothers being full sisters. In ten F_2 broods of hybrids between these subspecies, but of other parentage,[1] as well as in three F_3 broods and a number of back-crosses with pure races, no single instance has been observed. The most plausible guess, at present, is that we have to do with a simple recessive character. Fortunately, the two "albinic" mice are of opposite sex, so it is not unlikely that a test of this point will be practicable.

Since the weaning of these two "albinic" young, their mother, mated to the same father, gave birth to two more offspring, both pigmented. Thus, of the six derivatives of this pair of animals, two were albinic, and four normal. Or, counting the brood of five, borne by the other sister, we have four albinos in a total of eleven young. This excess over the expected ratio for a recessive character has, of course, little significance where the numbers are so small.

I am aware of no case in which complete or partial albinism has appeared as a result of the crossing of two strains which were not known to carry this defect, and it is quite possible that in the present instance the association of this phenomenon with subspecific hybridization is purely accidental. On the other hand, hybridization may, as has been contended, tend to call forth germinal disturbances, independently of ordinary Mendelian segregation.

As stated above, no evidences of simple monohybrid segregation have

[1] That is, other parentage on *both* sides. The father was used with various females but no albinos appeared except among the offspring of the two mothers here considered.

appeared among the normal F_2 hybrids between these two races of Peromyscus, though I am not yet prepared to report on this phase of the subject.

A YELLOW RACE OF *P. M. GAMBELI*

In September, 1914, a young female of *Peromyscus maniculatus gambeli* was trapped by me on the grounds of the SCRIPPS INSTITUTION, the appearance of which was so exceptional that the skin was saved. The pelage was still juvenal, but instead of having the usual dark gray tone, characteristic of this race in early life, it was relatively very pale. It is hardly possible that the strain described below is descended from the foregoing individual, though both may have had common ancestors within a very few generations.

In the spring of 1916, three peculiarly colored mice were found among the La Jolla *gambeli* stock of the second cage-born generation ("C_2," in my notation). They are of a peculiar yellow-brown hue, probably lying between the "cinnamon buff" and the "clay color" of RIDGWAY, and not unlike the most highly colored parts of the hair in *P. m. sonoriensis*. They differ from the latter race, however, in that this richer color covers the entire dorsal and lateral surfaces, instead of being confined to certain areas.[2] Proximally, the hairs are all of the normal slaty hue. Although no considerable attention was devoted to the first three of these "mutants" until the assumption of the colored pelage, it was noted in at least one case that the latter was preceded by an exceptionally pale juvenal coat.

These "yellow" *gambeli* contrast strongly with the brownish gray characteristic of the normal adults of this subspecies. Indeed, as already said, they diverge more widely from the typical condition of their own subspecies than do mice of a quite distinct subspecies. Thus far very few mice have been observed which show anything approaching an intermediate coat color. The existence of a few animals of somewhat intermediate appearance must be admitted, however, as well as the fact that the "yellows" themselves are far from being absolutely identical in color. The failure to report such departures from the "expected" condition of rigid distinctness is doubtless partly responsible for certain extravagances of neo-Mendelian speculation.

Upon looking over the pedigree of these first three "yellows," it was found that they were the offspring of three different mothers (C_1♀6, C_1♀7 and C_1♀77), and of two different fathers (C_1♂7 and C_1♂49),

[2] The color is purest, it is true, on the head and lateral surfaces, the dorsal region being finely streaked with black.

none of which exhibited the peculiarity. It is noteworthy that these three females and two males were all the offspring of a single pair of grandparents (♀46 and ♂16). Besides these five, there were no other offspring of this pair (see figure 1).

Of the two grandparents, one was trapped in the immediate vicinity of the SCRIPPS INSTITUTION, another at a point about a half mile distant. These mice were themselves killed for measurement before the peculiar condition of their descendants was realized. It may be safely assumed, however, that any such condition in the wild progenitors would have been noticed. All of the C_1 and C_2 representatives of this strain have been kept for further breeding purposes, and some other "yellows" have resulted.

At the time of writing, the total number of broods born of the five C_1 mice listed above, is eight. The number of individuals surviving to an age at which the detection of this color peculiarity was possible was eighteen. Of these, twelve were of the normal color and six of the aberrant.[3] Thus far, only four of the latter have matured sufficiently to show the definite yellow color of the adults, but this "mutation" appears to be nearly as recognizable in the juvenal as in the post-juvenal condition. In the former state the shade is much paler than the "deep neutral gray," which is characteristic of perhaps the majority of normal young *gambeli*, the difference between the two being most pronounced on the head. In these respects the young "yellows" reared in the laboratory agree closely with the young wild female mentioned at the opening of this section.

In contrast to the proportion of "yellows" appearing in this particular descent line, it must be mentioned that not a single other case has come to light among the four hundred or more cage-born *gambeli* which have been reared to maturity at La Jolla, since the commencement of the experiment. Moreover, with the single exception referred to at the beginning of this section, and a very few which are of somewhat intermediate appearance, no mouse resembling the yellow strain has been noted among the hundreds of these mice which have been trapped locally by my assistants and myself during the past two years.

Only two matings have been consummated in the case of the "yellows" themselves. The seven resulting offspring, while in the juvenal pelage, have agreed in being decidedly paler than the average young *gambeli* of this stage, the body shade being near the "light grayish olive" of

[3] The birth of another brood (C_1 ♀6 × ♂49) on March 2, 1917, raises these figures to 14 normal and 7 yellow.

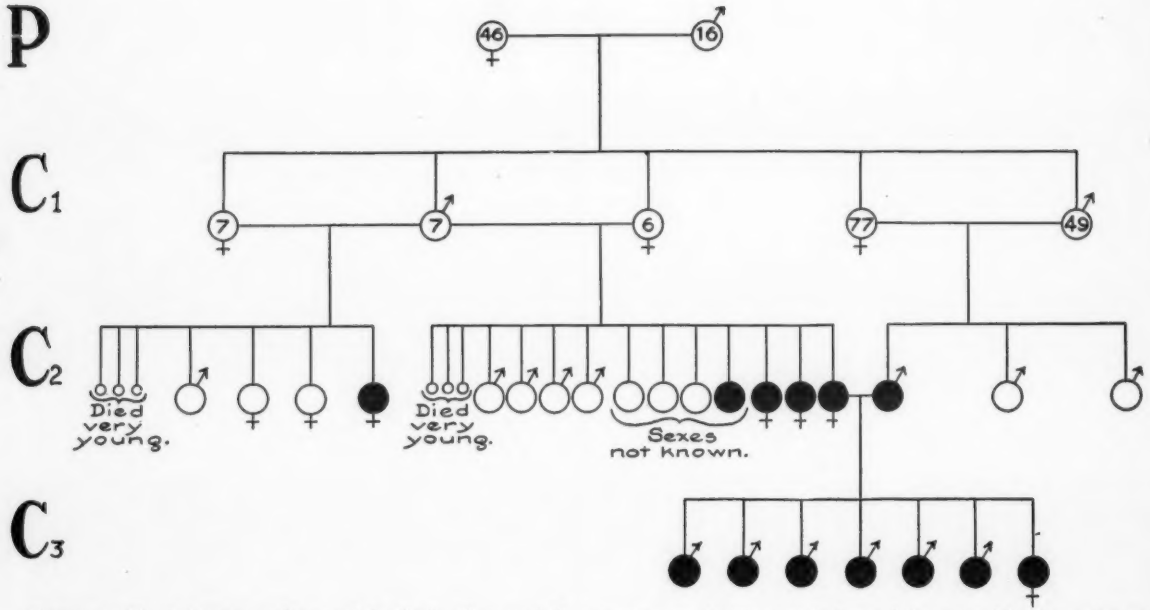

FIGURE 1.—Chart showing pedigree of the "yellow" race of *Peromyscus maniculatus gambeli* now being reared by the writer at the SCRIPPS INSTITUTION. P denotes the original wild parents. C_1, C_2 and C_3 denote the first, second and third cage-born generations. Yellow individuals are designated by circles of solid black, normal ones by open circles. The small circles denote mice whose nature was not determinable, owing to early death.

RIDGWAY, instead of the "deep neutral gray," and that of the head still lighter. On the other hand, they have certainly been darker than were some of the young "yellows" of the preceding generation, and have not been much paler than some exceptional individuals of the normal strain.

At the date of writing, the first-born of the two foregoing (C_3) broods is about four months old, and the three young mice are in the completed post-juvenal pelage. In this second pelage, they are nearly or quite as pale as the yellows of the "C_2" generation, and differ rather widely from most *gambeli* of their age. On the other hand, they lack, to a large degree, the richer color of the parents, having, in comparison with the latter, a decidedly "washed out" appearance. The divergence from the normal condition is thus less marked in the younger generation than in the older, and this difference between the two is probably not a matter of age.[4]

If we may disregard these possibly significant differences between the C_3 young and their more brightly colored parents, the facts suggest that this aberrant color is a recessive character, dependent on a single factor (or lack of one). Unless I have been a witness to the origin of a *bona fide* mutation, rather than a simple case of gametic segregation, we must suppose that one or both of the grandparents were heterozygous for this character. The five C_1 individuals must all have chanced to be heterozygous, a coincidence, to be sure, for which the chances would have been only one in thirty-two. The ratio 12:6, in the C_2 generation, does not, of course, depart significantly from the "expected" 12:4. In view of the small numbers, the difference may well be accidental.

The question of a possible relation between this "mutation" and the one first discussed is a matter of some interest. To consider only the conditions of pelage color, it might be supposed that the difference was merely one of degree. In the mature state, the one stock is a dark yellow, the other a very pale yellow, in the early life, one is medium gray, the other very pale gray. Some might perhaps suspect that the difference could be accounted for in terms of "intensity factors" or the like. But there would still remain differences between the two strains which could hardly be thus explained, viz., the presence and the absence of the tail-stripe, and the difference in the color and size of the eyes, the latter being quite normal in the "yellows." Without further data, any attempt at a factorial interpretation would of course be premature.

The fact that one of the "mutants" was trapped in nature is of some

[4] The second brood from the same parents approaches the yellow color more nearly. [Note added April 17, 1917.]

interest, since it shows that in this case at least, we are not dealing with a product of artificial conditions. CASTLE (1916, p. 124) states that "yellow sports" have been found among wild meadow-mice (Microtus) by COLE, BARROWS, F. SMITH and others. Apparently these have never been reared.

SPECIAL MARKINGS

Various peculiarities in the distribution of pigment in the skin or hair have been observed in individuals of all of my subspecies. Thus the white "star" on the top of the head has been noted in both *gambeli* and *sonoriensis,* some other tufts of white hair on the head of *sonoriensis,* a white terminal segment in the normally black caudal stripe of *rubidus,* as well as peculiarities in the skin pigmentation of the tail and snout of the last-named subspecies and of the feet in all three. Judging from what we know of various other animals, we might confidently predict that some or all of these aberrations would be "genetic."[5] Indeed, the mode of inheritance of these various peculiarities might prove as worthy of investigation as most of the other subject matter of recent Mendelian investigation.

Since the present studies are only incidentally concerned with the search for "mutations," or an inquiry into their mode of transmission, I can say little as yet regarding the inheritance of these special color markings in Peromyscus. In at least two cases, however, there are good reasons for believing that the markings in question are hereditary.

Before discussing the first of these cases, it must be stated that all of the subspecies of *Peromyscus maniculatus* have what is called a "bi-colored" tail, i.e., one in which the hairs of the dorsal surface are dark, while those of the ventral surface are white. Thus there is normally a sharply defined dorsal tail-stripe, varying in width according to the race and the individual.

Now a very few cases have been noted in *P.m. rubidus* in which this stripe terminated in advance of the distal end of the tail, i.e., the terminal portion was white dorsally as well as ventrally. One instance was that of a female of the wild stock trapped near Eureka, California, in which about 2 cm of the dark stripe was lacking. Of the five offspring of this mouse by a normal male, one (a male) showed this character quite clearly, the dorsal tail-stripe terminating about 5 mm in advance of the end (excluding the "pencil").

[5] CASTLE (1916, p. 125) states that "the production of white-spotted races from small beginnings . . . has been accomplished in the laboratory by CASTLE and PHILLIPS in the case of Peromyscus. . . ."

Besides this female, no other wild mouse showing this character has been found among about 250 *rubidus* which I have trapped. But among the first cage-born generation, three others appeared in addition to the male referred to in the preceding paragraph. These last, it is worth noting, were all offspring of a single pair (♀ 40 × ♂ 15). A fourth mouse of the same parentage was indeterminate in respect to this character, owing to the loss of the tip of the tail early in life. Neither of the parents was recorded as showing this peculiarity, and it is quite unlikely that it would have been overlooked, unless present to a very inconspicuous extent.

If this character is determined by a single "factor," the latter seemingly cannot be a dominant one. If recessive, we must suppose that the mate of the P_1 generation female first mentioned chanced to be heterozygous for this character; also that both parents of the second brood mentioned were heterozygous.[6] In the latter case, the number of recessive offspring ($\frac{3}{4}$ and possibly $\frac{4}{4}$) is much greater than the expectation, though it is needless to say that such small numbers prove nothing whatever. Indeed, it would be premature to assume a conformity with Mendelian ratios of any sort.

In relation to this aberrant tail character, it is of interest to note that LLOYD (1912, especially pp. 47, 112-116) records the occurrence of a similar condition in the house rat in India, and that he gives evidence for the existence of much restricted local strains in which this character has arisen more than once through independent mutations.

One further peculiarity of an apparently hereditary nature was found in ten or twelve specimens of the first cage-born generation of the subspecies *rubidus*. This was a white tip at the end of the snout, due to the absence of skin pigment as well as to the presence of white hairs. This character, with two doubtful exceptions, was found only among the progeny of two females (P♀40 and 41), by a single male (P♂15). It is noteworthy that ♀ 40 and ♂ 15 were the parents of three of the mice with white-tipped tails, and that these three all displayed the snout peculiarity as well as that of the tail. On the other hand, the fourth C_1 mouse having a white-tipped tail had a normally pigmented snout, showing that the two pigment defects are not inseparable.

Unfortunately none of the four C_1 *rubidus* with white-tipped tails has left descendants,[7] so that the further study of this peculiarity is, for the time being, prevented.

[6] Unless, indeed, we have to do with the *de novo* appearance of a real mutation.

[7] Save one in which the tail condition is indeterminate.

About ten cases of white-tipped snouts have appeared in the C_2 generation, and the relationships of these animals implies that this character depends primarily upon genetic conditions. But whether the character is dominant or recessive, or whether it depends upon one or more factors cannot be settled without giving more attention to the matter than at present seems warranted.

LITERATURE CITED

CASTLE, W. E., 1912 On the origin of an albino race of deer mouse. Science N.S. **35**: 346-348.

1916 Genetics and eugenics. pp. vi. + 353. Cambridge: Harvard University Press.

LLOYD, R. E., 1912 The growth of groups in the animal kingdom. pp. 185. London; Longmans, Green & Co.

MORGAN, T. H., 1911 The influence of heredity and of environment in determining the coat colors in mice. Ann. N. Y. Acad. Sci. **21**: 87-117. 3 colored pls.

CROSSING OVER WITHOUT CHIASMATYPE?[1]

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In a recent number of this journal Professor RICHARD GOLDSCHMIDT has a paper (1917), *"Crossing over ohne Chiasmatypie?"*, in which he develops a hypothesis to account for crossing over without recourse to the chiasmatype theory of JANSSENS (which, according to GOLDSCHMIDT, "ziemlich in der Luft schwebt"), or to any similar process.

The argument is based on the "von jedermann anerkannten Voraussetzungen der Chromosomenlehre." Among these Voraussetzungen GOLDSCHMIDT includes the idea that the chromosomes lose their structure during the resting stages, so that it is necessary that the particles be reassembled later to form the chromosomes seen at mitosis. It need hardly be pointed out that this view is not entirely established. Among others, the studies of JÖRGENSEN (1913), BOVERI (1909), BONNEVIE, VEJDOVSKY, and of the students of the "pro-chromosomes," make it at least open to serious doubt. Yet this idea forms the basis of GOLDSCHMIDT's whole argument, for it is assumed that the same mysterious "Kraft" is responsible for the rebuilding of the chromosomes and for crossing over.

However this may be, there are certain points in the further development of GOLDSCHMIDT's hypothesis that seem to me to call for even more critical examination than do his cytological considerations.

On p. 83 he says: "Es ist aber doch klar, dass man jede Proportion geometrisch als Entfernungen auf einer Geraden darstellen kann," and if this representation agrees with the facts, it shows only "dass irgendwelche Kräfte im Spiel sind, deren relativer Effekt als Entfernungen auf einer Geraden dargestellt werden können." Of course any series of proportions can be represented geometrically as sections of a single straight line; but only in certain special cases will such a representation show the relation of the parts to each other. In GOLDSCHMIDT'S own imaginary case (pp. 90-91) the relations are not fully represented by placing the

[1] Contribution from the Zoölogical Laboratory of Columbia University and the Carnegie Institution of Washington.

factors in a straight line. The factors *I* and *F*, for example, might be interchanged without appreciably affecting the degree to which the ratios fit. It may perhaps be surmised that the same sort of juggling can be done just as easily with the actual data on which the chiasmatype hypothesis of crossing over is based. This is not the case. In the first place, GOLDSCHMIDT has used for comparison only the data from the first paper developing the linear arrangement idea in detail (STURTEVANT 1913), although these data were at the time stated to be inadequate for certain loci, and have been supplemented by two more recent and extensive tabulations (STURTEVANT 1915, MORGAN and BRIDGES 1916).[2] Many of the inconsistencies pointed out by GOLDSCHMIDT and by the writer (STURTEVANT 1913), disappear when these later figures are used.

In the second place, the evidence which really puts the linear arrangement and chiasmatype theories on a sound basis is that obtained from experiments involving three or more loci at the same time. This phase of the matter is dismissed by GOLDSCHMIDT with two short paragraphs and a passing reference to the important work of MULLER (1916). These two paragraphs contain calculations for an imaginary experiment involving three loci, *B*, *D*, and *C*. The table on p. 91 gives the observed single crossover values for these three loci as follows:

$BD = 22.9 \quad DC = 13.0 \quad BC = 25.5$

GOLDSCHMIDT states, without giving the derivation of the result, that if the three loci are followed in one experiment the result will be:

Non-crossovers	67%
BD singles	20%
DC singles	10%
BDC doubles	3%

If we ignore for the moment the information gained by including *D* in the experiment, the observed crossovers between *B* and *C* will be $20 + 10 = 30$. But *BC* has just been stated to give 25.5. If it is intended to imply that heterozygosis for *D* affects the result, the only comment necessary is that the facts show no such relation to exist. As a matter of fact the values for the *BDC* experiment should read:

(I)	Non-crossovers	69.3%
(II)	*BD* singles	17.7%
(III)	*DC* singles	7.8%
(IV)	*BDC* doubles	5.2%

[2] One of these appeared over a year before GOLDSCHMIDT's manuscript was received, the other a few months before.

These figures and only these, will satisfy the conditions that

(a) I + II + III + IV = 100.0
(b) II + IV = 22.9 (*BD* crossovers)
(c) III + IV = 13.0 (*DC* crossovers)
(d) II + III = 25.5 (*BC* crossovers)

GOLDSCHMIDT declines to discuss the double crossover data further "weil wir glauben dass die STURTEVANT'schen Vergleichszahlen auf Grund einer falschen Formel berechnet sind, und sodann weil es . . . gar nicht unsere Absicht ist, das hier benutzte Schema an Stelle des MORGANschen setzen zu wollen."

I am unable to understand the bearing of the last part of this statement. It hardly seems necessary to point out that there is *a priori* no reason why a chiasmatype hypothesis should be the only possible explanation of the facts; and there would seem to be no point in developing any particular explanation, unless for the purpose of seeing if that explanation fits the known facts. GOLDSCHMIDT develops his speculation in great detail, until he comes to the really crucial evidence in favor of a chiasmatype view, and then the discussion is dropped. The statement that my formula (for expected number of double crossovers) (STURTEVANT 1915, p. 242) is incorrect seems a scarcely sufficient justification for ignoring that evidence, unless we are told how and why the formula is incorrect. The "formula" in question, when put in terms of symbols, states simply that if a crossover in region *AB* occurs in *p* (a fraction) of the cases, and a crossover in region BC occurs in *q* of them, then if the two crossovers are independent they will occur simultaneously (double crossover *ABC*) in p × q of the cases. This seemed to me to be a perfectly obvious application of an elementary principle of probability, and still seems so in spite of GOLDSCHMIDT's statement that he believes it to be incorrect.

By the use of this simple "formula" it has been found that the crossovers are in fact *not* independent, but that one crossover tends to prevent the occurrence of another one near it. By the same method it has been shown (see especially MULLER 1916) that large pieces of the chromosomes stick together, and *larger* pieces than would be expected as mathematical consequences of the single crossover values. These facts have been emphasized as forming perhaps the strongest evidence in favor of a chiasmatype hypothesis; in fact, they have been used to disprove the supposition "that at a resting stage the chromosomes go to pieces, and the fragments come together again before the next division period.

Linkage might then [be supposed to] mean the likelihood of fragments remaining intact, etc." (MORGAN, STURTEVANT, MULLER and BRIDGES 1915, p. 134). GOLDSCHMIDT, in effect, denies these facts *in toto*. Under the circumstances it seems natural to expect some cogent reason to be given for this denial. No explanation of linkage can have any claim to serious consideration unless it accounts for these facts.

LITERATURE CITED

BOVERI, TH., 1909 Die Blastomerenkerne von *Ascaris megalocephala* und die Theorie der Chromosomenindividualität. Arch. f. Zellforsch. **3**: 181-268. Pls. 7-11.

GOLDSCHMIDT, R., 1917 Crossing over ohne Chiasmatypie? Genetics **2**: 82-95.

JÖRGENSEN, M., 1913 Zellenstudien. I. Morphologische Beiträge zum Problem des Eiwachstums. Arch. f. Zellforsch. **10**: 1-126. Pls. 1-12.

MORGAN, T. H., and BRIDGES, C. B., 1916 Sex-linked inheritance in Drosophila. Carnegie Inst. Washington, publ. 237. 88 pp. 2 pls.

MORGAN, T. H., STURTEVANT, A. H. MULLER, H. J., and BRIDGES, C. B., 1915 The mechanism of Mendelian heredity. xiii + 262 pp. New York: Henry Holt & Co.

MULLER, H. J., 1916 The mechanism of crossing over. Amer. Nat. **50**: 193-221, 284-305, 350-366, 421-434.

STURTEVANT, A. H., 1913 The linear arrangement of six sex-linked factors in Drosophila, as shown by their mode of association. Jour. Exp. Zoöl. **14**: 43-59.

1915 The behavior of the chromosomes as studied through linkage. Zeitschr. f. ind. Abst. u. Vererb. **13**: 234-287.

NUMERICAL EFFECTS OF NATURAL SELECTION ACTING UPON MENDELIAN CHARACTERS[1]

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The relation of recent work in genetics to the Darwinian theory is still in dispute. The value of the natural selection hypothesis can only be determined by appropriate experimental tests. At present there appears to be no *inherent* incompatibility between DARWIN's fundamental principles and the newer concepts of pure lines, mutations, and unit characters. To some the action of natural selection seems to furnish an explanation of the actual trend of organic evolution which is lacking in later theories.

The "pure line" concept does not assist materially in explaining the existing diversity of species. If a pure line remain unchanged indefinitely it is difficult to account for the host of pure lines that exist at present. If, on the other hand, a real variation can occur in a pure line now and again, natural selection would help to explain the trend toward *adaptive* characters which these lines exhibit.

The "mutation" concept may represent the actual nature of variation better than the Darwinian notion of small fluctuating changes. Yet this scarcely affects DARWIN's main contentions. The *magnitude* and *frequency* of the variations are relatively unimportant, since in any case such variations will accumulate in the course of generations. Their *adaptiveness,* however, is highly significant for biology, and the question remains whether adaptive variations can sort themselves out from non-adaptive by the mere working of natural selection, without the action of a vital force or entelechy.

Finally, the Mendelian concept of "unit characters" in no way precludes the action of natural selection. Indeed it would seem to render easier the submission of the natural selection hypothesis to a crucial experimental test.

It should be noted, however, that the method generally employed in genetic work is not "natural" but "artificial" selection. Experimental-

[1] Written in connection with a course delivered in the Department of Psychology at the Johns Hopkins University.

ists have not generally attempted to measure the relative viability of individuals possessing alternative characters, perhaps the most distinctive feature of Darwinism. In order to determine whether (or to what extent) natural selection is an integral factor in evolution it would seem necessary to observe the changes from generation to generation in the relative proportion of the individuals bearing alternative characters, in a representative population living under natural conditions, and compare the outcome with the effects of natural selection as obtained by calculation. The result should determine whether natural selection actually works, or whether it is masked or assisted by other factors.

The writer has calculated the theoretical effects of natural selection upon pairs of alternative characters for two special cases. It is assumed (1) that one character is the Mendelian dominant, the other the corresponding recessive; (2) that individuals of one type die off more slowly than those of the other, owing to natural selection, but that neither type is wholly eliminated in each generation.[2] (3) The general formula would have to consider all degrees of fertility and all ratios of comparative viability between the alternative types. The present calculation assumes *one* fixed rate of reproductive increase only, namely a tendency to double the population within each "generation," and *two* special cases of relative viability—one in which the *dominant is twice as viable as the recessive,* and the other in which the *recessive is twice as viable as the dominant.*

By hypothesis, natural selection occurs only when one of the alternative forms is more adapted to the environment than the other. It is assumed in this discussion that greater *adaptiveness* means greater *viability* or fitness to survive, and that therefore a measure of adaptiveness may be obtained by comparing the numerical proportion of each class in successive generations.

(4) So long as the environment can support the growing population the element of competition plays a minor rôle. But as the population approaches the limit of numbers which the environment will support, competition becomes more intense and adaptiveness becomes more and more of a factor in determining survival. It is assumed that the limit of population which the given environment will support is reached at G_0; our calculation begins at this point.

[2] So far as the writer is aware, previous calculations along these lines deal only with cases in which one form is selected and the other wholly eliminated. (See, e.g., JENNINGS, H. S., "Numerical results of diverse systems of breeding," GENETICS **1**: 65, 1916.)

Case 1. Dominant fitter. In table 1 it is assumed that the limit of population is 2048 individuals, and that when this limit is reached in G_0 the pure dominants (*AA*) number 512, the mixed dominants (*Aa*) 1024, and the pure recessives 512. It is assumed further that these forms are all equally reproductive, that the population tends to *double* in each generation, and that the recessives are only *half as viable* (under competitive conditions) as the dominants (whether pure or hybrid).

By pure chance mating, the number of individuals produced in G_1 will be 1024 *AA*, 2048 *Aa*, and 1024 *aa*. But of these half will die before reaching the mating stage, and the loss of *aa's* by hypothesis will be twice as great (in proportion to their numbers) as the loss of *AA*'s or *Aa*'s; that is, the loss of *aa*'s will be 819, of *Aa*'s 819, and of *AA*'s 410.[3] This loss is readily calculated by adding together the number of *AA*'s plus the number of *Aa*'s plus twice the number of *aa*'s and dividing the sum into the limit of population; this gives the "factor of loss" for each of the dominant forms; for the recessive this factor is multiplied by 2.

For example:

	G_1	G_2
	$1024 + 2048 + 2 \times 1024 = 5120$	$1474 + 1966 + 2 \times 656 = 4754$
Factor of loss	$= 2048 \div 5120 = 0.4$	$2048 \div 4754 = 0.431$
Whence, loss of *AA*'s	$= 1024 \times 0.4 = 409.6$	$1474 \times 0.431 = 635.274$
" " *Aa*'s	$= 2048 \times 0.4 = 819.2$	$1966 \times 0.431 = 847.346$
" " *aa*'s	$= 1024 \times 0.8 = 819.2$	$656 \times 0.862 = 565.472$

Subtracting the loss from the number of individuals produced in each case we find the number of *reproducing* individuals of each sort in G_1, which are given under G_1', and so for each generation. For example:

	G_1	G_1'
AA	$1024 - 410 = 614.$	

In order to determine the number of individuals produced in any generation we first find the number of *A* and *a* gametes in the "surviving" individuals of the preceding generation; thus, the number of *A* gametes = twice the *AA* individuals + the *Aa* individuals; the number of *a* gametes = twice the *aa* individuals + the *Aa* individuals. Now by chance mating the number of *AA* individuals in the next generation is proportional to the square of the *A* gametes in the preceding, the number of *aa* individuals is proportional to the square of the *a* gametes, and the number of *Aa* gametes is proportional to twice the product of *A* and *a*,—the simple binomial formula. But by hypothesis the actual number

[3] The fractions in the tables are given as the nearest unit. It is found that these slight deviations average up, reducing the error to negligible size in the long run.

TABLE I

Case 1: In which the dominant form is fitter to survive.

	G_0	G_1	Loss	G_1'	G_2	Loss	G_2'	G_3	Loss	G_3'
AA	512	1024	410	614	1474	635	839	1910	868	1042
Aa	1024	2048	819	1229	1966	847	1119	1774	806	968
aa	512	1024	819	205	656	566	90	412	374	38
Factor of loss:			.4			.431			.454	
Gametes:										
A	2048			2457			2797			3052
a	2048			1639			1299			1044

	G_4	Loss	G_4'	G_5	Loss	G_5'	G_6	Loss	G_6'
AA	2274	1068	1206	2560	1226	1334	2780	1348	1432
Aa	1556	730	826	1356	650	706	1189	577	612
aa	266	250	16	180	172	8	127	123	4
Factor of loss:		.4695			.479			.485	
Gametes:									
A			3238			3374			3476
a			858			722			620

	G_7	Loss	G_7'	G_8	Loss	G_8'	G_9	Loss	G_9'
AA	2950	1442	1508	3084	1515	1569	3192	1574	1618
Aa	1052	514	538	940	462	478	848	418	430
aa	94	92	2	72	71	1	56	56	0
Factor of loss:		.4888			.4913			.493	
Gametes:									
A			3554			3616			3666
a			542			480			430

	G_{10}	Loss	G_{10}'	G_{11}	Loss	G_{11}'
AA	3281	1623	1658	3351	1660	1691
Aa	770	381	389	708	351	357
aa	45	44	1	37	37	0
Factor of loss:		.4945			.4955	
Gametes:						
A			3705			3739
a			391			357

AA = pure dominant; Aa = hybrid; aa = recessive.

G_1, etc. = number produced; G'_1, etc. = number which survive and reproduce.

Assumptions: (1) Population tends to double in each generation; (2) Limit of support is reached at 2048; (3) Recessives are half as viable as dominants.

of individuals produced is twice the number of the producers. Hence we divide each result by the factor 4096 (i.e., the total number of producing gametes, since this has been squared.)

For example:

G_1' gametes	G_2 individuals
$A^2 = (2457)^2 = 6036849$	$AA = 6036849 \div 4096 = 1473.84$
$2Aa = 2 \times 2457 \times 1639 = 8054046$	$Aa = 8054046 \div 4096 = 1966.32$
$a^2 = (1639)^2 = 2686321$	$aa = 2686321 \div 4096 = 655.84$

Repeating this calculation for successive generations (table 1) we find that the pure recessives tend to disappear in 8 generations, that is, the number produced is so small that less than $\frac{1}{4096}$ reach the reproducing age. The number of hybrids also steadily diminishes, and in the 11th generation amounts to only 0.211 of the pure dominants.

Case 2. Recessive fitter. In table 2 the same assumptions are made, excepting that the recessives are assumed to be twice as viable as the dominants. The calculations are the same, except that here the factor of loss is $AA + Aa + \frac{1}{2}\ aa$, divided into the limit of population.

For example: in G_2, $753 + 2006 + 668.5 = 3437.5$

Factor of loss $= 2048 \div 3427.5 = 0.598$

TABLE 2

Case 2: In which the recessive form is fitter to survive.

	G_0	G_1	Loss	G_1'	G_2	Loss	G_2'	G_3	Loss	G_3'
AA	512	1024	585	439	753	450	303	488	311	177
Aa	1024	2048	1170	878	2006	1199	807	1851	1178	673
aa	512	1024	293	731	1337	399	938	1757	559	1198
Factor of loss:			.5719			.598			.636	
Gametes:										
A	2048			1756			1413			1027
a	2048			2340			2683			3069

	G_4	Loss	G_4'	G_5	Loss	G_5'	G_6	Loss	G_6'
AA	258	179	79	96	75	21	19	17	2
Aa	1539	1070	469	1062	828	234	514	455	59
aa	2299	799	1500	2938	1145	1793	3563	1576	1987
Factor of loss:		.695			.7796			.8848	
Gametes:									
A			627			276			63
a			3469			3820			4033

	G_7	Loss	G_7'	G_8	Loss	G_8'
AA	1	1	0	0	0	0
Aa	124	120	4	8	8	0
aa	3971	1927	2044	4088	2040	2048
Factor of loss:		.97			.998	
Gametes:						
A			4			0
a			4092			4096

AA = pure dominant; Aa = hybrid; aa = recessive.

G_1, etc. = number produced; G'_1, etc. = number which survive and reproduce.

Assumptions: (1) Population tends to double in each generation; (2) Limit of support is reached at 2048; (3) Recessives are twice as viable as dominants.

Whence, loss of AA's $= 753 \times 0.598 = 450.294$
Aa's $= 2006 \times 0.598 = 1199.588$
aa's $= 1337 \times 0.299 = 399.163$

The reproducing population of each sort (*AA, Aa, aa*), and the numbers of each sort produced in the next generation, are obtained precisely as in case 1.

It is found that the elimination proceeds much more rapidly in case 2, the pure dominants being practically wiped out in the 7th generation and the dominant gametes disappearing entirely in the 8th, so that the selection is then complete.

It is obvious that if the rate of reproduction is greater than the rate assumed here (i.e., doubling between successive generations), the progress of elimination will be more rapid, and conversely if the rate of reproduction is less. Also, if there is a greater difference in viability of dominants and recessives than the ratio here assumed (2 : 1), the elimination will proceed more rapidly, and conversely. Professor H. S. JENNINGS has indicated to the writer a method of extending the calculation to cover *all* cases by means of a general formula.[4]

Assume:

(1) That the population at the beginning has reached the limit of numbers that can survive; and call this survival number n.

(2) The population increases in a constant ratio, such that at each change of generations it becomes l times as great as before.

(3) The viability of the dominants is to that of the recessives as m to 1. That is, the dominant survives m times as readily as the recessives. (m may be greater or less than unity.)

(4) Let the population at the beginning consist of $r\,AA + s\,Aa + t\,aa$.

Now, after one reproduction the population will be ln. Since it must be reduced again to n, there must be lost $(l - 1)n$ individuals.

These are to be divided between r, s, and t in the proportions $r : s : mt$ (since t dies m times as readily as the others).

Then the total number of r that die (out of the entire $(l - 1)n$ deaths) will be:

$$\frac{r}{r + s + mt} \times (l - 1)n = \frac{rn(l - 1).}{r + s + mt}$$

Similarly the number of s that die will be:

$$\frac{sn(l - 1)}{r + s + mt}$$

[4] Professor JENNINGS is responsible for the following discussion (as far as the summary). The writer gratefully acknowledges his kindness in permitting its inclusion here.

The number of t that will die:

$$\frac{mtn(l-1)}{r+s+mt}$$

These values may then be subtracted from r, s, and t respectively to give r, s, and t, the numbers perishing after the selection has occurred.

Then the proportions for r, s, and t in the next generation may be obtained from the following formula:[5]

$$AA = (s+2r)^2$$
$$aa = (s+2t)^2$$
$$Aa = 2(s+2r)(s+2t)$$

Example.—Case 1: Dominant fitter to survive; generation, G_1.

Here $n = 2048$
$l = 2$
$m = 2$
$r = 1024$
$s = 2048$
$t = 1024$

And $l - 1 = 1$

$$r + s + mt = 5120 \quad (=5\times 1024)$$

Then:

$$r' = 1024 - \frac{1024 \times 2048}{5 \times 1024} = 1024 - 409.6 = 614.4$$

$$s' = 2048 - \frac{2048 \times 2048}{5 \times 1024} = 2048 - 819.2 = 1228.2$$

$$t' = 1024 - \frac{2 \times 1024 \times 2048}{5 \times 1024} = 1024 - 819.2 = 204.8$$

Case 2 is identical, save that $m = 1/2$ instead of 2; so that $r + s + mt = 3584$ (or 7×512).

SUMMARY

It is found that, assuming a greater adaptation of one Mendelian alternate, either the dominant or the recessive, the more adaptive form tends gradually to "drive out" the less adaptive. The rate of elimination depends on the relative viability of the two forms, as well as on the rate of reproduction of the species. But *the elimination is more rapid when the recessive form is the more viable.*

Adaptiveness may be explained *without the assumption of any in-*

[5] JENNINGS, H. S., 1916, Numerical results of diverse systems of breeding. GENETICS **1**: See p. 65.

herent orthogenetic tendency, if adaptive variations occur as well as non-adaptive. Assuming that by some means real heritable (i.e., mutational) variations *do* occur, whether they be large or inappreciably small, the result in the long run is to select those which fit the species to cope with its environment and to eliminate those which place their possessors at a disadvantage.

It remains to test experimentally whether and to what extent such variations actually occur, and whether the working of natural selection (as above assumed) is masked or reinforced by other more potent factors.